

A revision of *Brillantaisia* (Acanthaceae)

KAREN SIDWELL

Department of Botany, The Natural History Museum, Cromwell Road, London SW7 5BD

CONTENTS

Introduction	68
Taxonomic history	68
Morphology	69
Habit	69
Indumentum	71
Cystoliths	71
Stem	71
Wood anatomy	71
Leaves	71
Inflorescence	74
Bracts and bractlets	74
Calyx	74
Corolla	74
Androeceium	76
Pollen	76
Gynoeceium	76
Fruit	76
Seeds	76
Concepts of species and higher taxa	76
The species of <i>Brillantaisia</i>	78
Relations of the species of <i>Brillantaisia</i> 1: formulation of the data matrix	78
Choice of outgroup	78
Choice of characters	78
The data matrices	78
Relations of the species of <i>Brillantaisia</i> 2: analysis of the data matrix	78
Results	79
Taxonomic account	83
Key to fertile specimens of <i>Brillantaisia</i>	83
Nomen dubium	105
Species transferred to <i>Hygrophila</i>	106
Species transferred to <i>Eremomastax</i>	106
References	106
Exsiccatae	107
Systematic index	113

SYNOPSIS. *Brillantaisia* P. Beauv. is a genus of mainly woody herbs and subshrubs from tropical Africa and Madagascar. In this revision, a brief taxonomic history of *Brillantaisia* is presented, the morphological variation of the genus is described, and concepts of species and higher taxa are discussed. The Phylogenetic Species Concept of Nelson & Platnick is adopted as the criterion for species delimitation whilst hennigian monophyly is the criterion used for recognition of higher taxa. Twelve species of *Brillantaisia* are delimited. The relations between the twelve species of *Brillantaisia* and eleven outgroup species representing the genera, *Duosperma*, *Dyschoriste*, *Eremomastax*, *Hygrophila*, *Mellera* and *Mimulopsis*, are investigated using cladistic methodology and a phylogeny is presented. The results of cladistic analysis show that *Brillantaisia* and six species of *Hygrophila* both belong within a monophyletic group based on a suite of pollen characters. *Brillantaisia* is a monophyletic genus based on the laterally compressed upper corolla lip, membranous hinge at the apex of the corolla tube and winged petiole. *Hygrophila* is paraphyletic, and until further studies are undertaken on that genus, the sister group to *Brillantaisia* remains unresolved. Within *Brillantaisia*, section *Stenanthium* of Lindau is monophyletic; however, subgeneric taxa are not formally recognized in this treatment. A taxonomic account of the twelve species of *Brillantaisia* is provided with illustrations, distribution maps and a key. The main taxonomic changes are that *B. stenopteris* is new to science; *B. riparia* is raised from a variety of *B. pubescens* to species level; *B. grottanellii* is recognized as distinct from *B. madagascariensis*; *B. kirungae*, *B. ulugurica* and *B. cicatricosa* are considered conspecific and *B. owariensis* is circumscribed as a single widespread and variable species.

XX (312094.1)

INTRODUCTION

The aim of this paper is to present a revision of *Brillantaisia* with a key for identification of species, addressing the following questions:

1. How many species are there in *Brillantaisia*?
2. Is the genus *Brillantaisia* monophyletic?
3. Are the subgeneric groups within *Brillantaisia* proposed by Lindau (1895a) monophyletic?
4. Is *Hygrophila* the sister group to *Brillantaisia*?
5. Is *Hygrophila* monophyletic?

Brillantaisia P. Beauv. is a genus of mainly woody herbs and shrubs from tropical Africa and Madagascar. Plants of *Brillantaisia* generally have ovate leaves with a winged petiole, an open panicle inflorescence of bilabiate purple flowers and capsules containing numerous seeds, each held on a hooked retinacula. At the outset of this study, there was no consensus concerning the delimitation of *Brillantaisia*, species boundaries within the genus or species relationships. The genus was thought to contain between 13 (Vollesen, pers. comm.) and 40 (Mabberley, 1987) species. The monospecific genus *Plaesianthera* (C.B. Clarke) Livera from Sri Lanka had recently been transferred to *Brillantaisia* as an Asian representative of the genus by Cramer (1991); however, this genus has been shown to be best placed within *Hygrophila* R. Br. (Sidwell, in press a) and is not discussed further in this paper. Prior to undertaking cladistic analyses, *Brillantaisia* is hypothesized as monophyletic (*sensu* Hennig, 1950, 1979), based on the presence of two posterior stamens, two staminodes and a laterally compressed upper corolla lip; the genus *Hygrophila* is hypothesized as the sister group to *Brillantaisia* based on previous classifications of Nees (1847), Bentham (1876), Lindau (1895a) and Bremekamp (1953, 1965), and the monophyly of the taxon Hygrophileae containing only *Brillantaisia* and *Hygrophila*, is provisionally accepted on the presence of four aperturate pollen (Scotland, 1992a, b, 1993; Furness, 1994) and a unique ndhF sequence (Scotland et al., 1995).

Taxonomic history

Brillantaisia was first described in 1818 by Ambroise Marie Palisot de Beauvois from a collection made near Agathon in Benin, West Africa (Palisot de Beauvois, 1818). A single species, *Brillantaisia owariensis* P. Beauv., was described as having a four angled stem, violet flowers in a panicle and ovate-lanceolate toothed leaves with an acute tip and a winged petiole. Thirty years later, Nees von Esenbeck (1847) overlooked the original publication of *Brillantaisia* and described two new genera of Acanthaceae from West Africa: *Belantheria* Nees and *Leucoraphis* Nees. Bentham (1849) recognized the oversight of Nees and transferred the two species of *Leucoraphis* to *Brillantaisia* as *B. lamium* (Nees) Benth. and *B. vogeliana* (Nees) Benth. and synonymized *Belantheria belvisiana* Nees with *Brillantaisia owariensis*. In 1853, Hooker addressed the already problematic issue of species delimitation in *Brillantaisia*. He agreed with Bentham (1849) that the three species described by Nees (1847) should be placed within *Brillantaisia*; however, after observation of a newly introduced garden plant from Sierra Leone (Lindley, 1853), Hooker (1853) concluded that the separation of those species on leaf margin and leaf shape characters was invalid as the character variation previously used to distinguish between the

species could be seen on a single cultivated specimen. Hooker therefore united all the species recognized by Nees (1847) and Bentham (1849) under the earliest name, *Brillantaisia owariensis* P. Beauv.¹.

Since that time, many new species of *Brillantaisia* have been described (see Sidwell, 1997 for detailed discussion). Gustav Lindau was by far the most prolific describer of new species in the genus. Between 1893 and 1904 Lindau published descriptions of 25 new species of *Brillantaisia*. The first, largest and possibly most important of these publications was *Acanthaceae Africanae I* (Lindau, 1893), in which, ten new species of *Brillantaisia* were described. Characters used by Lindau at the species level included habit (herb or shrub), leaf shape (ovate or obovate), leaf base shape (cordate or not cordate), leaf apex shape (acuminate or not), cystoliths (present or absent), whole plant indumentum (pubescent or glabrous), sepal length (equal or unequal) and number of ovules. By the time of his account of Acanthaceae in Engler and Prantl's *Die Natürlichen Pflanzenfamilien* (Lindau, 1895a) Lindau had published fourteen names in *Brillantaisia*, and was the first and only worker to delimit subgeneric taxa within the genus. Lindau subdivided *Brillantaisia* into two sections: three species with spicate inflorescences were included in section *Stenanthium* Lindau, and nine species with panicle inflorescences were mentioned in section *Euryanthium* Lindau. Section *Euryanthium* was further subdivided on leaf shape characters into Group A with lanceolate leaves (containing *B. lancifolia* Lindau) and Group B with non-lanceolate leaves (containing all other species with a panicle inflorescence).

Brillantaisia is now generally considered to be more closely related to the genus *Hygrophila* R. Br. than to other members of the Acanthaceae because both genera possess a bilabiate corolla and numerous seeds. However, historically, the position of *Brillantaisia* within the Acanthaceae has been somewhat confused. Nees von Esenbeck (1847) was the first to produce a worldwide monograph of the Acanthaceae. He refined his work on Asian Acanthaceae (Nees, 1832), changing the rank of some taxa, and placed both *Brillantaisia* (as *Belantheria* and *Leucoraphis*) and *Hygrophila* in the subfamily Echinacanthaceae (possessing retinacula), tribe Hygrophileae (corolla 5-parted; stamens 2 or 4; seeds numerous; fruits explosive), Subtribe 1. This was the first grouping of *Brillantaisia* and *Hygrophila* in the same taxon. However, in the same year Lindley (1847) listed *Brillantaisia* as of unknown affinity and noted that three eminent botanists working on the Acanthaceae – Brown, Nees and Meisner – were unable to agree on subdivision of the family. Lindley (1847: 679) noted that 'there are few natural Orders which now demand, in so eminent a degree, a searching investigation as that of Acanthads'. Bentham (1876) subdivided the Acanthaceae into five tribes using a combination of characters (corolla aestivation, ovule number, seed shape and retinacula type). *Brillantaisia* and *Hygrophila* were placed in tribe Ruellieae Benth. (aestivation contorted; seeds 2-many per locule; seeds laterally compressed; retinacula hooked), subtribe Hygrophileae (corolla two-lipped; filaments laterally connate). Baillon (1891) recognized six series in Acanthaceae and considered *Brillantaisia* sufficiently distinct to be placed in the monogeneric series Brillantaisiées characterized by the presence of two fertile posterior stamens, a strongly bilabiate corolla and many seeds per capsule.

The research of Lindau (1895a) placed *Brillantaisia* and

¹ There remains some confusion here as Hooker did not explicitly state that *Belantheria* Nees and *Leucoraphis* Nees (separated on the presence or absence of staminodes) should be united under one species of *Brillantaisia*. Typographic error increases the confusion as two species of Bentham (1849), *Brillantaisia lamium* and *Brillantaisia vogeliana*, are apparently mis-named by Hooker (1853), as '*Belantheria lamium*' and '*Belantheria vogeliana*', two combinations which had never been formally published prior to that work. The lumping of *Brillantaisia lamium*, *B. vogeliana* and *B. owariensis* by Hooker is not upheld in this work. Although leaf margin characters are very variable within the genus, there are other discrete morphological characters supporting the recognition of these three species as distinct.

Hygrophila in the Acanthoideae-Contortae-Hygrophileae having 'rippenpollen' with four equatorial apertures. Bremekamp (1965) also placed *Brillantaisia* with *Hygrophila*, in Acanthoideae-Ruellieae-Hygrophilineae, a group with bilabiate flowers in cymes, stamens united into a single group, style not held in place by a row or bundles of trichomes and subglobose, banded, usually four-aperturate pollen. As mentioned above, recent studies confirmed the monophyletic nature of the group consisting of these two genera based on a pollen type not found elsewhere in Acanthaceae (Scotland, 1993) and a unique ndhF sequence (Scotland et al., 1995).

Since the time of Nees von Esenbeck (1847) no monographic work has been undertaken for *Brillantaisia* and the prolific description of species by Lindau (1893; 1894; 1895*a, b, c, d*; 1896; 1897; 1898; 1904) served to exacerbate difficulties in understanding the group. Several regional floras (Heine, 1966; Benoist, 1967; Champluvier, 1985; Vollesen, in prep. *a & b*) have addressed the problem of the number of species within *Brillantaisia* in Gabon, Madagascar, Rwanda and East Africa respectively. The authors of these works disagree in particular on the number of species in several morphologically distinct groups within *Brillantaisia*. Taxonomists working on *Brillantaisia* have tended to split it into poorly defined groups and formally name many slightly differing forms of the great morphological variation within the genus. Many new species of *Brillantaisia* have been described, often from little material and based on characters that are highly variable within the genus. Identification of specimens has been inconsistent and a study covering the entire range of geographical and morphological variation of the genus is essential to clarify this confusion.

MORPHOLOGY

Initially I considered it impossible to separate description of the morphological variation of *Brillantaisia* from discussion of the transformation of that information into comparative morphological data (characters and character states) for phylogenetic analysis. However, morphological data are analysed at two different levels in this study. Characters and character states of individual specimens are analysed when delimiting species of *Brillantaisia*, and characters and character states of taxa are analysed when forming hypotheses of relations among those species. In order to emphasize the filtering of data undertaken when transforming observation and description into comparative data, a descriptive approach to discussion of characters is presented prior to discussion of character coding for cladistic analysis. A purely descriptive morphological section provides an overview of the genus, directly comparable with many published monographic studies and some flora accounts for the Acanthaceae, recent examples of which include studies on *Justicia* (Graham, 1988), *Justicia* sect. *Harnieria* (Hedrén, 1989), *Justicia* sect. *Ansellia* (Ensermu, 1990), *Ruellia* (Ezcurra, 1993), *Strobilanthes* (Wood, 1995), *Dicliptera* (Balkwill et al., 1996) and *Phalopsis* (Manktelow, 1996). Brief discussion of morphological variation is given here and species that exhibit the range of variation of a particular organ are used as examples. Herbarium specimens relevant to the discussion are referenced by collector's name, number and herbarium acronym (e.g. *Kibwua* 5191, UPS).

The data were obtained through observation of herbarium specimens from BM*, BR*, C, DSM*, E*, ETH, FHO*, G, HBG, K*, LISC, M, MHU, MO*, NY, P*, PRE, S, SCA*, SRGH, W, WAG*, YA* and Z (abbreviations follow Holmgren et al., 1990). Visits have been made to the herbaria marked with an asterisk. Gross morphological features were measured on mature vegetative and reproductive

structures using a mm ruler or calipers which measure to 0.1 mm. Finer measurements were made using an 8 mm 0.1 graticule in a Leica Wild M8 dissecting microscope. Floral dissections were made after placing a flower into cold water and heating slowly until the water almost boiled. This usually took about 30 seconds and was sufficient to soften the delicate corolla. Boiling caused the corolla to disintegrate. Photographs were taken using a Nikon F-801s camera with FP4 black and white film and a Microtech MF80 fibre optic light source. Pollen preparations were acetolysed using a modification of Erdtman (1960) (see Sidwell, 1997). Light micrographs of pollen grains were taken using a Dialux 20EB photomicroscope. Scanning electron micrographs were taken at The Natural History Museum, London. Stubs were coated in gold-palladium 80:20% and viewed using an Hitachi S-800 SEM microscope with a working distance of 5–10 mm. Permanent slides of *Brillantaisia* wood were prepared according to Gourlay (pers. comm.): the stem was boiled for an hour, cut in transverse, tangential longitudinal and radial longitudinal sections on a sliding microtome and stained in safranin. The sections were passed through a dehydration series, washed three times in alcohol and mounted in Canada balsam.

Habit

Brillantaisia species range in habit from delicate herbaceous *Brillantaisia lancifolia* Lindau, approximately 50 cm high, to the large woody species *B. kirungae* Lindau which reaches 7 metres tall. Within this range, *Brillantaisia* species are mainly erect, perennial herbs around 1.5 metres tall which often become woody at the base of the stem. *Brillantaisia lamium*, *B. vogeliana* and *B. madagascariensis* T. Anderson ex Lindau, for example, are all erect, perennial herbs that produce adventitious roots at the lower nodes or along branches that touch the ground, enabling them to spread vegetatively. The terms herb, shrub and tree have been loosely applied by collectors to describe the habit of *Brillantaisia* species. For example, *B. madagascariensis* ranges in habit from a 'soft succulent herb' (Mooney 6071, S) or a 'perennial herb with creeping and ascending stems' (Friis & Vollesen 613, C) to a 'shrub to 2m tall' (*Kibwua* 5191, UPS). According to the model of plant architecture, described by Weberling (1989) after Troll (1964), plants can be divided into four distinct and clearly defined zones: main florescence; enrichment zone; inhibition zone and innovation zone. This model was used by Manktelow (1996) in her monograph of *Phalopsis* and can be applied to species of *Brillantaisia* (Fig. 1).

Figure 1 illustrates the architecture of *Brillantaisia* from the apex to the base of the plants as follows. The inflorescence is divided here into two distinct and more precisely defined parts: the terminal thyrse with lateral dichasial branches forms the main florescence and flowering lateral branches (coflorescences) which 'repeat the structure of the main axis to some extent' (Weberling, 1989: 225) form the enrichment zone. These two parts are separated from one another by the basal internode (bi on Fig. 1), and the whole flowering region is termed a synflorescence. Below the enrichment zone, where the axillary buds do not develop into coflorescences, is the inhibition zone, and below that, the region of vegetative growth is termed the innovation zone. The innovation zone is considered the region of production of new shoots after flowering in perennial plants. *Brillantaisia lamium*, *B. vogeliana*, *B. owariensis* and *B. madagascariensis* all exhibit the type of growth pattern described above and illustrated in Figure 1A. Two species, *B. lancifolia* and *B. debilis* Burkill have a main florescence and lack the enrichment zone (Fig. 1B). In the annual species, *B. pubescens* T. Anderson ex Oliv. inhibition of the lateral shoots does not occur, lateral coflorescences occur to the base of the plant and the inhibition and innovation zones

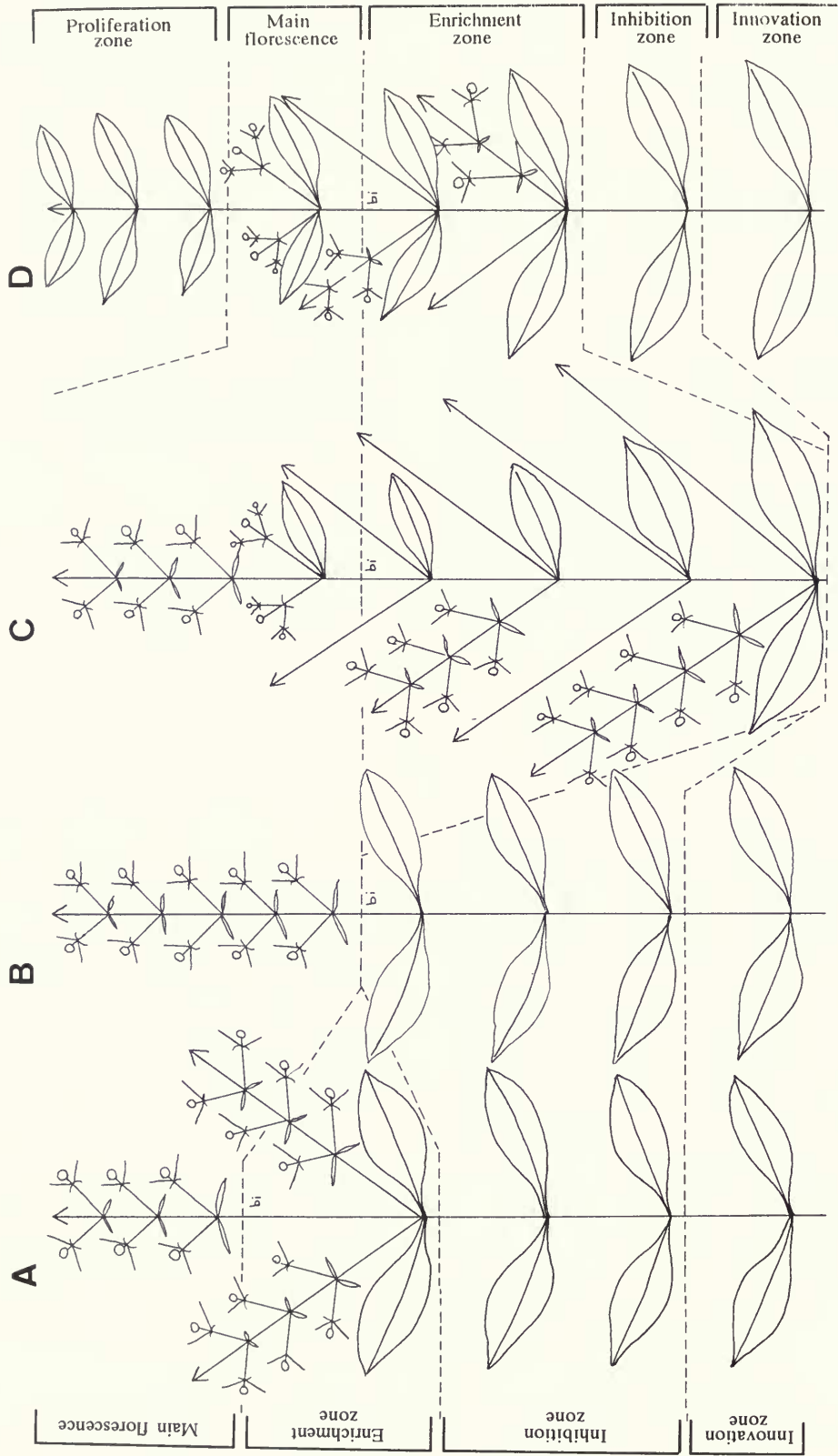


Fig. 1 Models of the architecture of *Brilliantaisia* species. A. The model of Troll (1964) and Weberling (1989) with four zones, separated by dashed lines: the main florescence; enrichment zone; inhibition zone and innovation zone; B–D modifications of A; B lacking an enrichment zone; C. lacking inhibition and innovation zones; D with a proliferation zone above the main florescence.

are absent (Fig. 1C). In two species of *Brillantaisia*, the main axis of the plant continues to grow vegetatively above the flowering region. This phenomenon is termed proliferation. Troll (1964) considered the type of vegetative growth seen in *B. oligantha* Milne-Redh. and occasionally in *B. riparia* (Vollesen & Brummitt) Sidwell to be late proliferation which 'consists of the return of the inflorescence apex to a vegetative condition' (Weberling 1989: 257; Fig. 1D). The robust *Brillantaisia kirungae* has been described as a 'very large, straggling, bushy herb' (Ball 62, SRGH), a 'robust subshrub' (Bridson & Lovett 544, MO) or even a 'small tree' (Thomas 3790, MO; White 13908, FHO). White's description of *B. kirungae* includes bole measurements which clearly indicate that the plant is a tree, 4 m high with a trunk 1.4 m tall and 12 cm in diameter at 70 cm height (White, 1984); however, such accurate measurement and application of terminology is unusual. I was unable to study this species in the field and the precise pattern of architecture of *B. kirungae* remains uncertain.

Indumentum

The variation of trichomes on different organs of Acanthaceae has been studied in some detail by previous researchers (e.g. Ahmad, 1976, 1978). Singh & Jain (1975) studied the structure and ontogeny of trichomes of Acanthaceae and classified them into forty types in two major groups: glandular and eglandular. Species of *Brillantaisia* possess both glandular and eglandular trichomes. Eglandular trichomes on *Brillantaisia* are of three types: simple filiform trichomes, three to nine cells long, tapering towards the apex; short uniseriate trichomes, two cells long, also tapering to the apex and unicellular trichomes with a rounded apex that is often purple. Glandular trichomes are stalked with a multicelled, capitate head (Selvaraj & Subramanian, 1983) and a two to many celled stalk. The number of cells in the head and stalk of glandular hairs varies continuously between organs and among individuals of *Brillantaisia*. Detailed discussion of indumentum types on the different parts of *Brillantaisia* plants is presented in Sidwell (1997).

Cystoliths

Calcium carbonate cystoliths are present in most members of Acanthaceae and were extensively documented in the last century by Hobein (1884). Recent studies by Inamdar et al. (1990) indicated that variation of cystolith morphology may be a useful taxonomic character above the generic level in Acanthaceae. The cystoliths of *Brillantaisia* are solitary, elongated and pointed at one end. All vegetative parts, bracts, bractlets and calyces are covered in this type of cystolith. The size of cystoliths in *Brillantaisia* varies intraspecifically and even within a single organ of one specimen.

Stem

In this work, the stem is treated as the axis of the plant below the main florescence and basal internode as shown in Figure 1 and is equivalent to the 'hypotagma' of Weberling (1989: 230). The stem is square towards the apex, longitudinally grooved on opposite sides and more rounded towards the base of the plant. The corners of the upper stem are usually slightly curved but may be sharply angled and winged. The stem is slightly swollen at or just below the nodes in all species. Below the basal internode the stem varies in diameter from 1–2 mm in *Brillantaisia debilis* to c. 10 mm in *B. kirungae*. In *B. madagascariensis*, *B. vogeliana* and *B. lamium* adventitious roots may be produced at the lower nodes. The epidermal stem surface is covered in cystoliths, oriented parallel to the stem. Multicellular trichomes which may be glandular or eglandular are present on the upper stem and are particularly dense at the nodes.

Wood anatomy

A review of the wood anatomy of 38 species of Acanthaceae was written by Carlquist & Zona (1988). No species of *Brillantaisia* or *Hygrophila* were included in his survey which concluded that 'Woods of Acanthaceae are characterized by relatively narrow vessels with simple perforation plates and alternate lateral wall pitting, septate libriform fibers, scanty vasicentric axial parenchyma, rays both multiseriate and uniseriate, erect ray cells abundant in rays ... numerous small crystals or cystoliths in ray cells ... and nonstoried structure' (Carlquist & Zona, 1988: 201). The stems of plants of *Brillantaisia* often become lignified at the base, particularly in *B. owariensis* and *B. kirungae*. Data on woodiness are very rarely collected on herbarium specimens. One specimen (Poulsen 523, FHO) included a collection of the lignified lower stem of *B. kirungae* 20 mm in diameter. This piece of stem showed a clear central pith with wood 7 mm thick and bark 1 mm thick. Transverse sections (Fig. 2A, B) show the vessels, which are relatively broad for the family, to be usually solitary and arranged radially with columns of parenchyma forming medullary rays between the regions of vessels. The vessels have simple perforation plates and minute pitting on the outer walls (Fig. 2F). The fibres are long, thin-walled, septate cells (Fig. 2C, E, F) between which are regions multiseriate rays characterized by a predominance of erect ray cells (Fig. 2C, D). Cystoliths are visible in ray cells but cannot be seen in the sections shown here.

Leaves

The leaves of *Brillantaisia* are characteristically ovate with a winged petiole. However, they vary enormously in size, shape, margin, the extent of the petiole wing and the distribution and density of trichomes on both surfaces. Leaf shape ranges from linear-lanceolate to broadly ovate (Fig. 3). The petiole may be unwinged, or winged to the base. The margin is often irregular, sometimes having dentate, crenate and serrate teeth and may be secondarily toothed. The leaf texture ranges from chartaceous in *B. vogeliana* to slightly coriaceous in *B. owariensis* and *B. kirungae*. The venation is eucamptodromous with tertiary veins becoming perpendicular to the midrib toward the apex of the leaf. In *B. kirungae*, the leaves often dry black. Some *Brillantaisia* species can be recognized to species level when sterile. For example, *B. lamium* has perhaps the most characteristic leaves of all the species, with a usually cordate leaf base, an entire margin and an unwinged petiole (Fig. 3A). *Brillantaisia lancifolia* has lanceolate, entire leaves (Fig. 3I). Plants of *B. madagascariensis*, *B. debilis*, *B. oligantha*, *B. pubescens* and *B. riparia* all possess entire-margined, ovate leaves with a cuneate leaf base narrowly tapering into a winged petiole (Fig. 3B, F, G, H, L). The species with toothed leaves are very variable and relatively difficult to distinguish from one another. Leaves of *B. vogeliana* can be easily recognized by the presence of irregular teeth on the petiole wing, particularly where it widens into the lamina base (Fig. 3C), and by the rather open tertiary venation with unclear quaternary veins. Leaves of *Brillantaisia kirungae* are also characteristically grossly, irregularly toothed (Fig. 3E) and have prominent horizontal and vertical tertiary and quaternary veins giving a very close squared pattern. The leaves of *B. owariensis* exhibit a large range of leaf size, shape and margin type (e.g. Fig. 3K). The leaves often have prominent, parallel tertiary veins running between the secondary veins, with the quaternary veins not clear. Unfortunately, herbarium specimens tend not to show the extent of variation of leaf size in the genus. *Brillantaisia kirungae* and some forms of *B. owariensis* have very large lower leaves which have rarely been collected as they do not readily fit into a plant press.

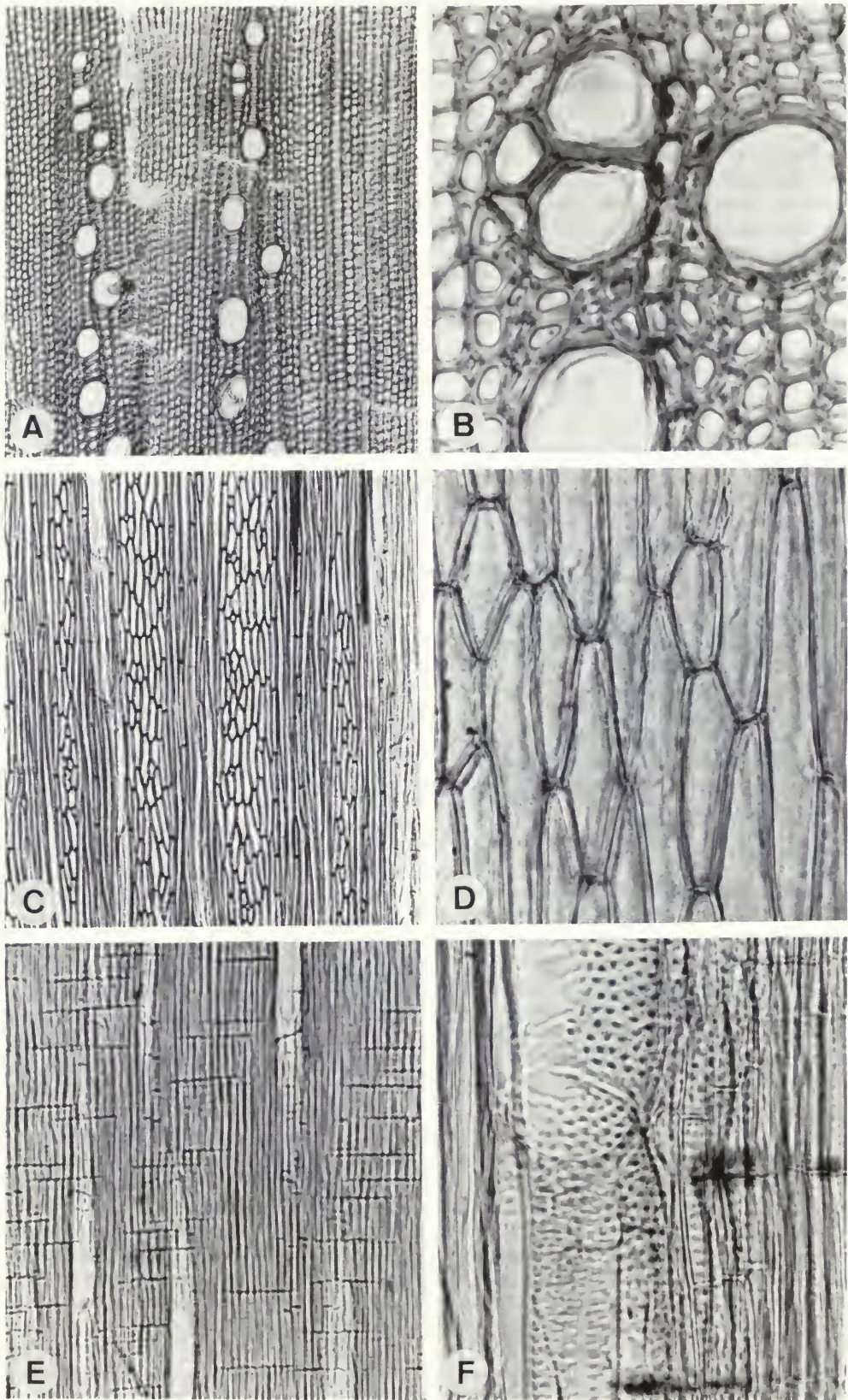


Fig. 2 Wood anatomy of *Brillantaisia kirungae* (Poulsen et al. 523, FHO, C, K). A. TS $\times 50$; B. TS $\times 250$; C. TLS $\times 50$; D. TLS $\times 250$; E. RLS $\times 50$; F. RLS $\times 250$.

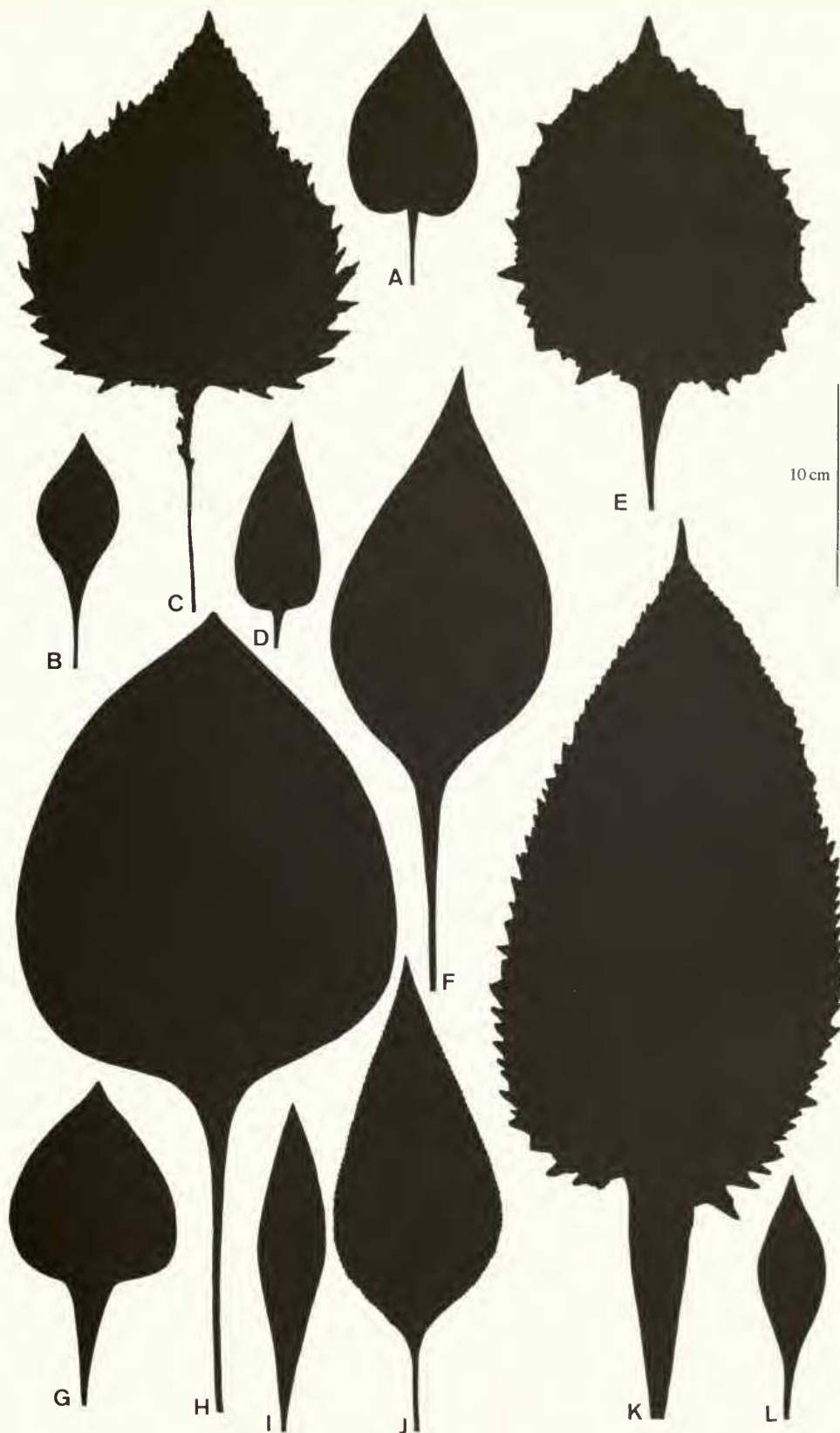


Fig. 3 Leaf shape variation in *Brillantaisia*. A. *Brillantaisia lamium* (Figuieredo & Arriegas 32, LISC); B. *B. debilis* (Louis 2161, WAG); C. *B. vogeliana* (Manktelow et al. 89, UPS); D. *B. lamium* (JFI 32657, MO); E. *B. kirungae* (Friis & Vollesen 58, C); F. *B. oligantha* (Brass 17042, MO); G. *B. madagascariensis* (Loveridge 71, MO); H. *B. pubescens* (Vollesen 2392, UPS); I. *B. lancifolia* (Talbot 200, BM); J. *B. grottanellii* (Ensermu & Zerihun 619, ETH); K. *B. owariensis* (Barbosa 1812, LISC); L. *B. riparia* (Robyns 151, BR).

Inflorescence

Brillantaisia inflorescences have been described in general terms as 'panicules' (Heine, 1966: 83), 'panicules terminales amples ou spiciformes, formes de cymes lâches ou contractées' (Benoist, 1967: 28) or 'large open or contracted panicles, rarely in spiciform racemes' (Vollesen, in prep. a). As with many genera of Acanthaceae, it is often difficult to pinpoint a precise division between the vegetative and floral parts of *Brillantaisia* plants and inflorescence structure and variation cannot be described by simply using the broad conventions of botanical terminology such as panicle, raceme, spike or cyme. Although several workers have studied the morphology of Acanthaceae inflorescences in detail, for example in the genera *Pseuderanthemum*, *Ruellia*, *Barleria* and *Lepidagathis* (Sell, 1969a), *Anisotes* (Baden, 1981), *Justicia* (Graham, 1988), *Duvernoia* and *Adhatoda* (Manning & Getliffe-Norris, 1985), *Ruellia* (Ezcurra, 1993), *Phalopsis* (Manktelow, 1996) and *Dicliptera* (Balkwill, 1996) and discussed the problem of appropriate descriptive terminology, there has been no attempt to reach a consensus regarding the application of terms to the inflorescences of Acanthaceae. Several of these studies (Baden, 1981; Manning & Getliffe Norris, 1985; Graham, 1988) illustrated and discussed modifications of different inflorescence types from an 'ancestral' compound dichasium via 'elaboration', 'reduction' and 'condensation' (Graham, 1988: 555). Hedrén's (1989: 20) terminology for *Justicia* sect. *Harnieria* attempted to 'find a simple and consistent terminology for supposedly homologous structures'. However, his terms were different from those previously used for *Justicia* or other Acanthaceae and have not been generally applied at that level. The lack of generally applicable terminology and the lack of parallel usage of available terminology has meant that the easiest solution for each botanist working on Acanthaceae inflorescences has been to develop his or her own clear, explicit terminology for a particular group of plants. *Brillantaisia* inflorescences are described below in light of both important general works on inflorescence morphology (Rickett 1944, 1955; Troll, 1964; Sell, 1969a; Weberling, 1989) and the studies of Acanthaceae mentioned above.

The model of the habit of *Brillantaisia* species described above (Fig. 1A) is used as a starting point for understanding inflorescence architecture. The habit model divides the inflorescence into a terminal, main florescence and a lower enrichment zone of lateral coflorescences, the whole flowering region of a plant being termed a synflorescence (Fig. 4A–F). The basic 'unit' of Acanthaceae synflorescences is the dichasium, described by Rickett (1944: 216) as 'a cluster formed by a dichotomy beneath a terminal flower' which 'in its simplest form consists of three flowers' (Fig. 4A). In *Brillantaisia* synflorescences, the basic dichasium structure is repeated and modified so that in most species the amount of dichasial and monochasial branching increases, more or less regularly, down the synflorescence from the apex (Fig. 4A & B). Following the terminology of Weberling (1989: fig. 109) the main florescence of *Brillantaisia* is usually a regular, dichasially branching thyrse or double thyrse (Fig. 4A). Below the main florescence, lateral coflorescences may be present (Fig. 4C). Plants of *B. madagascariensis* and *B. grottanellii* Pichi-Sermoli have very short lateral inflorescence branches, hence the spicate florescence on which Lindau based his sectional division of *Brillantaisia* mentioned above (Fig. 4D). The apex of the main florescence may return to indeterminate vegetative growth as in *B. oligantha* (Fig. 4E). In this case, the lateral dichasia are produced in the axil of a leaf rather than a bract and the question of whether the whole structure is the main florescence or a synflorescence of lateral dichasia arises once

again. Indeterminate main florescences may also have lower coflorescences as seen in *B. riparia* (Fig. 4F).

The development of a general terminology for Acanthaceae inflorescences to help clarify higher level homology assessment is considered essential, but beyond the boundaries of this study as it will require detailed ontogenetic, anatomical investigations across a wide range of taxa.

Bracts and bractlets

The bracts of *Brillantaisia* are paired at the nodes of the main florescence axis. In most species of *Brillantaisia* the bracts are foliose, becoming smaller towards the apex of the inflorescence. The bracts are often caducous, for example, *B. owariensis*, has large leaf-like bracts present in the young developing inflorescence which fall soon after the inflorescence opens. The bracts of *B. kirungae* are large, rounded at the apex, amplexicaul and pubescent with short trichomes. Amplexicaul bracts are not seen in other species of *Brillantaisia*. Hedrén (1989: 21) used the term bracteole to refer to 'small, narrow bracts', differentiating them from 'leaf-like bracts'. His terminology is considered imprecise as 'bracteole' specifically refers to 'a leaflike organ subtending a flower in an inflorescence that is itself subtended by a bract' (Blackmore & Tootill, 1984: 48) and does not refer to the size or shape of the organ. The bractlets of *Brillantaisia* do not subtend the flowers, but occur at the dichotomous branching of the dichasial florescence. The term bractlet is used (as by Daniel, 1984) in preference to the term bracteole and refers to the second, third or higher order leaf-like structures at the nodes of the lateral branches of the main florescence or coflorescences. The bractlets of most species of *Brillantaisia* are linear, sessile, and rounded at the apex. Plants of *Brillantaisia pubescens* have shortly petiolate, rounded bractlets which are persistent and highly characteristic of the species.

Calyx

The calyx of *Brillantaisia* has five linear or spatulate, pubescent sepals that are united at the base. The upper adaxial sepal is usually larger than the other four although *B. lamium* and some forms of *B. owariensis* have five subequal sepals. In *B. kirungae*, the upper sepal may be several times wider and longer than lateral sepals. Plants of *B. pubescens*, *B. riparia* and *B. vogeliana* have clearly spatulate sepals. During fruit maturation, the calyx may lengthen significantly. In *B. pubescens*, the largest sepal is as long as the fruit. In *B. owariensis* the upper sepal is occasionally much longer than the fruit.

Corolla

The corolla of *Brillantaisia* has left contort aestivation (Scotland et al., 1994) common to all members of the Contortae *sensu* Lindau (1895a). The two lipped corolla of *Brillantaisia* is highly characteristic of the genus. The corolla tube is cylindrical, the upper lip is hooded and strongly laterally compressed, the lower lip is usually reflexed with three lobes at the apex. Between the base of the lower lip and the corolla tube is a region of membranous folded tissue which acts as a hinge allowing the corolla lobes to pivot on the corolla tube presumably facilitating pollination. Corolla morphology varies in the length and width of the tube, the ratio of the tube to the lobes, the shape of the lower lip, and the pubescence of the petals (see Figs 8–16). Corollas range in colour from deep purple to pink with white forms found occasionally in *B. vogeliana*, *B. lamium* and *B. madagascariensis*. The West African white-flowered *B. madagascariensis* was previously recognized, on the basis of this character alone, as a separate species.

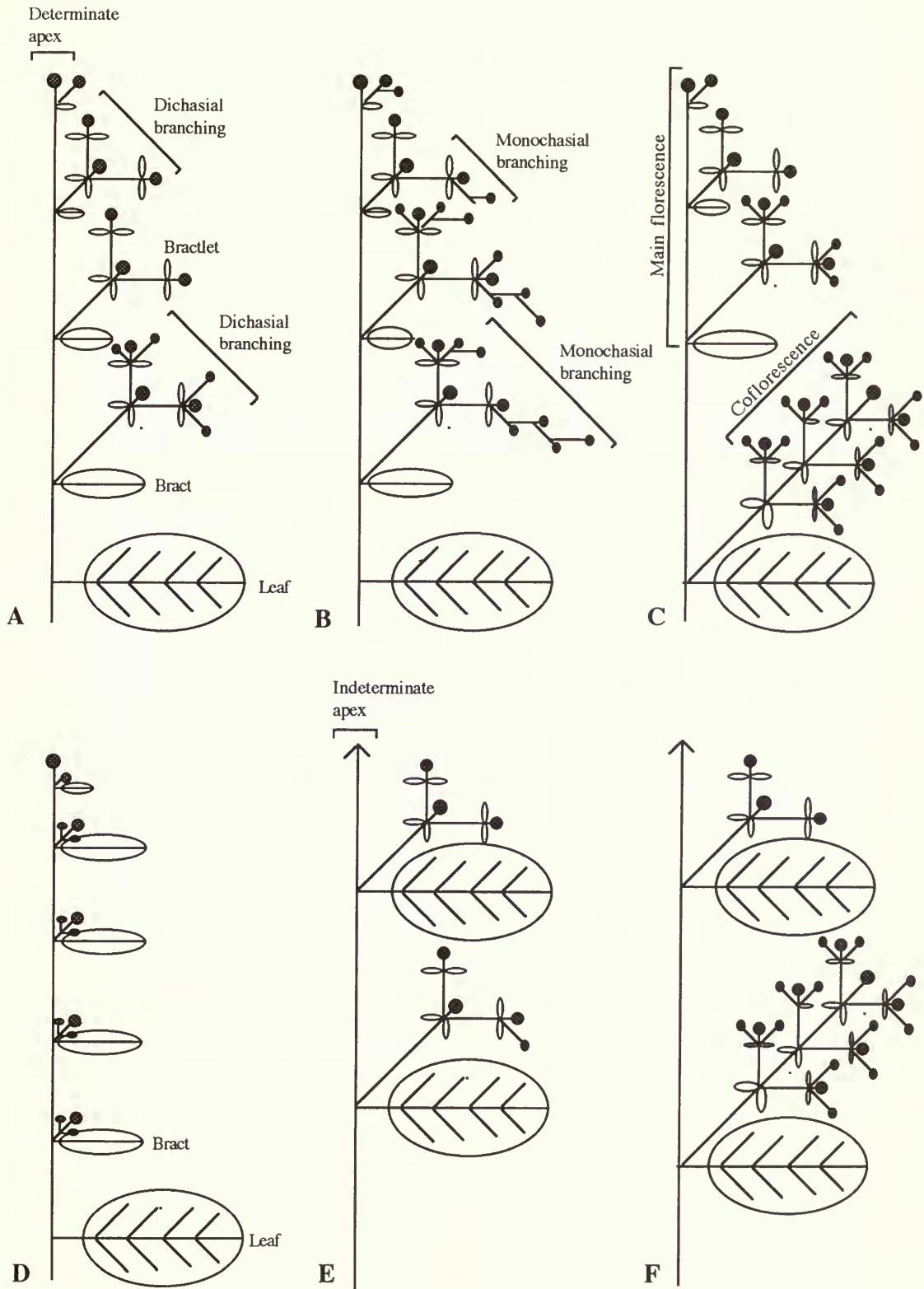


Fig. 4 Synflorescence structure of *Brillantaisia* species. A. basic structure of main florescence: determinate at the apex, with lateral branching once or twice dichasial; bracts on main axis foliose becoming smaller towards the apex, smaller foliose bractlets on lateral branches; B. main florescence with lateral branching both dichasial and monochasial; C. main florescence with lower lateral corymbes repeating the structure of the main florescence, the whole forming a synflorescence; D. main florescence with reduced lateral branches forming a spike with large persistent bracts; E. main florescence with indeterminate apex; F. main florescence with indeterminate apex and lower lateral corymbes.

Androecium

Species of *Brillantaisia* have two stamens and two staminodes. It is the two posterior stamens in *Brillantaisia* that are fertile, unlike other Acanthaceae with two stamens in which the anterior pair develop (e.g. Fig. 12C). This was mentioned by Lindau (1895a: 278) who stated 'Die Reductionen im Andröecium gehen stets so vor sich, dass die hinteren Stb. zuerst zu Staminodien werden oder ganz verschwinden, nur bei *Brillantaisia* finden sich ausnahmsweise die beiden vorderen Stb. zu Staminodien umgebildet'. The fertile anthers are symmetrical, sagittate, dorsifixed and dehiscent through long lateral slits. The filaments are flattened towards the base, narrowing towards the anther and are almost as long as the corolla lobes and held in the upper hooded lip. The staminodes usually extend beyond the corolla tube and have a small flattened vestigial anther at the apex. In *B. pubescens* (Fig. 8E), *B. riparia* (Fig. 9B) and *B. oligantha* (Fig. 10B) the staminodes are minute or absent.

Pollen

The pollen grains of Acanthaceae are very variable and have been used extensively in taxonomic research on the family (Radlkofer, 1883; Lindau, 1895a; Bremekamp, 1944; Raj, 1961; De, 1960; Immelman, 1989; Scotland, 1991, 1992a, b, 1993; Furness, 1994). The pollen of *Brillantaisia* is usually oblate spheroidal but ranges from suboblate to spheroidal (terms according to Punt et al., 1994). Lindau (1895a) used the term rippenpollen to describe the usually oval-ellipsoidal grains with pseudocolpi and equatorial apertures found in *Brillantaisia*. Pollen grains of *Brillantaisia* are four-aperturate (see Fig. 5 and plates in Furness, 1994). The apertures are compound colporate structures consisting of an elongated colpus with a circular endoaperturate pore in the centre. Between the four apertures are pseudocolpi, similar to the colpi but lacking an endoaperture. The number of apertures on a pollen grain occasionally varies and may range from four to six within a single sample. In one pollen sample of *B. owariensis* studied by Furness (1994) all the pollen grains had five apertures, but this character has not been consistently found in other samples of the same species or elsewhere in the genus. Scanning electron micrographs (Fig. 5) clearly show that *Brillantaisia* pollen has raised bands of tectum with pseudocolpi between these bands. The collumellae are fused into a distinct biretulate tectum in most species of *Brillantaisia* forming a primary reticulum with a smaller reticulate secondary tectum in the lumen (Fig. 5E). *Brillantaisia madagascariensis* has very characteristic pollen with irregularly clavate tectum ornamentation (Fig. 5A–C). *Brillantaisia grottanellii* is morphologically very similar to *B. madagascariensis*, however, investigation of pollen morphology showed this species to lack any tectal ornamentation (Fig. 5D–F). These data combined with gross morphological data, support recognition of *B. grottanellii* as a distinct species.

Gynoecium

The ovary of *Brillantaisia* species is cylindrical, 1–2 mm in diameter and up to 6 mm long and pointed at the apex, tapering to the base of the style (e.g. Fig. 9D). The ovary sits on an annular disc and has parietal placentation with two rows of ovules on each placental axis. *Brillantaisia* species have between twelve and sixty ovules in contrast to most other Acanthaceae which usually have just four ovules per ovary. The style is linear and with a small slightly flattened region at the apex forming the end stigma (Fig. 12D). Many species of Acanthaceae and related families have a simple bifid stigma whereas the second lobe of the stigma of *Brillantaisia* is reduced to a barely visible raised 'tooth' at the base of the receptive stigmatic surface.

Fruit

The fruit of *Brillantaisia* are dry, elastically dehiscent capsules with retinacula (Figs 8–16), characteristic of many members of the Acanthaceae (Sell, 1969b). The capsules are erect on the lateral synflorescence branches, each valve has a longitudinal groove from base to apex and within each valve, the seeds are held on two rows of dry, comparatively large, hook-shaped retinacula (Fig. 14A & E). The retinacula is a hardened outgrowth from the funicle of the developing embryo. The capsules of *Brillantaisia* are many seeded (Figs 8–16), compared to the capsules of most Acanthaceae which usually contain only 2 or 4 seeds. Often one or two ovules at the narrowed base or apex of the fruit do not develop into fully mature seeds. The fruit vary between species in size and the number of seeds per capsule and pubescence, for example: the fruit of *B. pubescens* are the smallest in the genus (Fig. 8F); plants of *B. vogeliana* have small fruit with up to 30 seeds per valve (Fig. 13A & C); plants of *B. kirungae* have large glandular pubescent fruit with 8–10 seeds per valve (Fig. 12E) and the fruit of *B. debilis* and *B. lamium* are glabrous (Figs 14A & 16C).

Seeds

Seed surface characters have been shown to be taxonomically useful at the species level in several groups of Acanthaceae including *Hypoestes* (Balkwill & Getliffe-Norris, 1985) and *Peristrophe* (Balkwill et al., 1986), and in the recognition of infrageneric taxa in *Justicia* (Immelman, 1990; Lester & Ezcurra, 1991) and *Siphonoglossa* (Immelman, 1990). The production of mucilage (myxospermy) is common in the Acanthaceae. The mucilage was considered by Kippist (1845) to come from pores in the ends of the seed trichomes. Grubert (1974) said the mucilage was produced by the seed coat.

The seeds of *Brillantaisia* were first described in detail by Schaffnit (1906). The seeds are flattened, asymmetrical, kidney-shaped and covered with long, hygroscopic trichomes which are adpressed when the seed is dry. When wet, the seeds produce mucilage and the hygroscopic trichomes rapidly expand. Trichomes of seeds of all *Brillantaisia* species are along, thin, single cell tapering towards and rounded at the apex with regular annular and occasionally spiral thickening from base to apex. Similar trichomes are common to all species of *Brillantaisia* and *Hygrophila* (Schaffnit, 1906), and were also reported in *Ruellia* by Kippist (1845).

CONCEPTS OF SPECIES AND HIGHER TAXA

The importance of explicitly stating the concepts and methods used for recognition of taxa in botanical monography was highlighted by Luckow (1995) and McDade (1995), among others, and has been discussed in relation to a revision of *Brillantaisia* in an earlier paper (Sidwell, in press b). Implicit taxonomic convention that the personal opinion of an expert botanist is sufficient to delimit taxa was deemed unacceptable for an unbiased scientific study of *Brillantaisia*. The literature on species concepts was carefully reviewed and evaluated and a brief outline of the conclusions of that paper is presented below. Above the level of species, relationships of higher taxa are hierarchical and all groups are recognized on the single criterion of Hennigian monophyly. Species are thought of as different from higher taxa and are delimited independently from considerations of monophyly and prior to any cladistic analysis. They are 'consistent with cladistic theory but independent of constraints of autapomorphy' (Nixon & Wheeler, 1990: 213) and can be

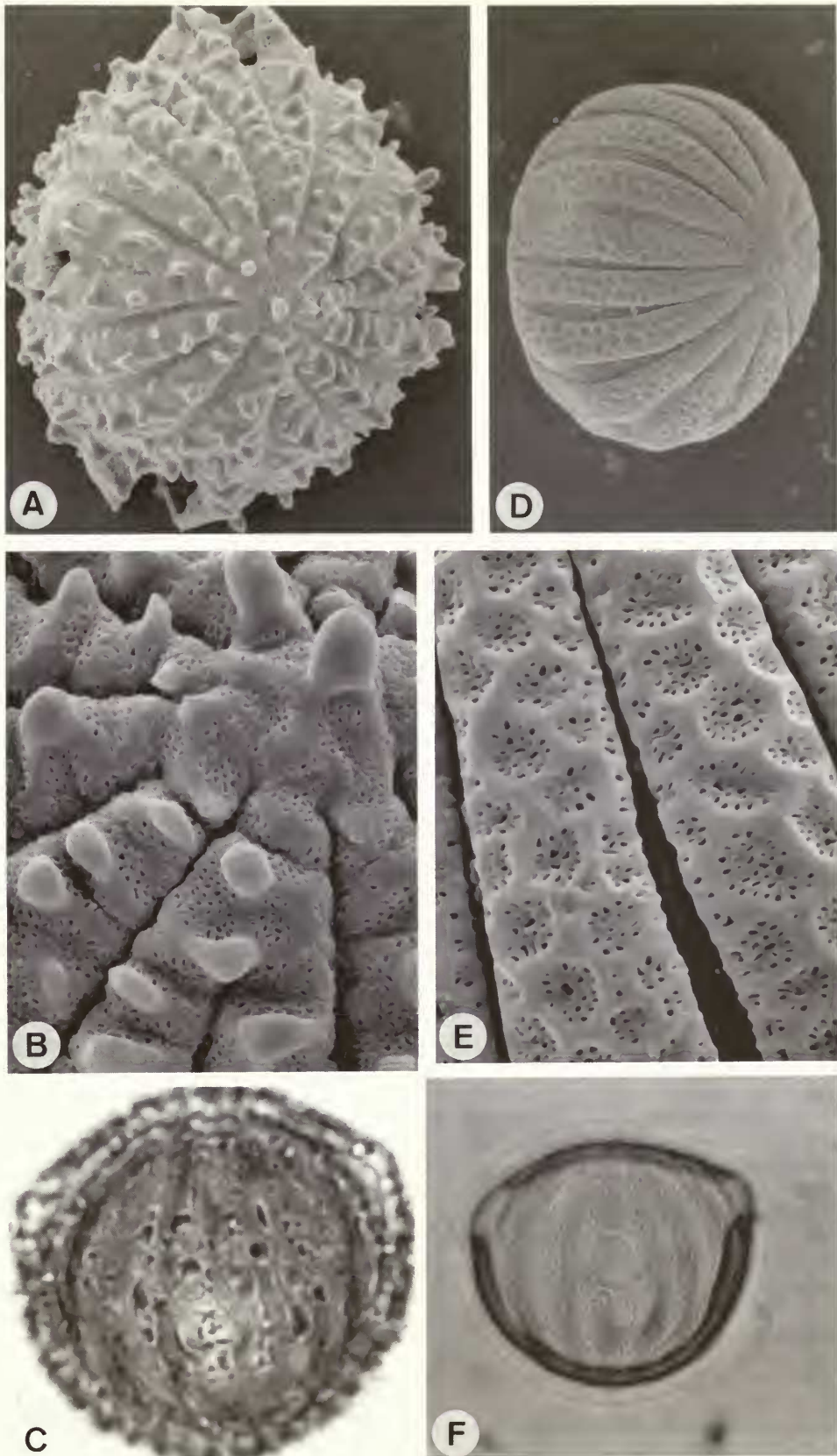


Fig. 5 The pollen of *Brillantaisia madagascariensis* and *B. grottanellii*. A–C *B. madagascariensis* pollen (Gutzwiler 841): A. SEM polar view $\times 1.5$ K; B. SEM close up of tectum $\times 7$ K; C. Light micrograph, equatorial view $\times 1$ K with clavate ‘spines’ on the tectum. D–F the smaller pollen of *B. grottanellii* (Ensermu et al. 821): D. SEM subpolar view $\times 1.5$ K; E. SEM close up of tectum $\times 7$ K; F. Light micrograph, equatorial view $\times 1$ K, with an even, non-spiny bireticulate tectum.

'recognized by either unique characters or unique combinations of characters' (Luckow, 1995: 595). Nelson & Platnick (1981) noted the fact that 'species' are only represented by the samples available to a particular biologist and that in practice 'those samples that a biologist can distinguish, and tell others how to distinguish (diagnose), are called species' (Nelson & Platnick, 1981: 11). However, they go on to point out that a pattern based species concept is incomplete without an element of process – that of self-perpetuation – and state that '... species are simply the smallest detected samples of self-perpetuating organisms that have unique sets of characters' (Nelson & Platnick, 1981: 12).

The species of *Brillantaisia*

Twelve species of *Brillantaisia* were recognized. All twelve species could be recognized on the presence of unique sets of morphological characters; however, two kinds of species group are present. Seven of these species are monothetic, possessing a single character diagnostic for that species group and five species polythetic, lacking any single diagnostic character. As well as falling within the definition of a polythetic group, defined by the possession of a unique set of characters, *Brillantaisia owariensis* could also be considered a widespread and variable 'ochlo-species' (Sidwell, 1997). The term *ochlo-species* was first coined by White (1962: 79) to describe three species of *Diospyros* (Ebenaceae) which are all widespread and 'have very complicated variation patterns'. White wrote 'Some of their variation is closely correlated with geography, but most of it is not, so that the pattern is of the checkerboard type discussed by Mayr (1942: 37) but more complicated than any of his examples. Such species cannot be satisfactorily subdivided and could conveniently be distinguished from monotypic and polytypic species by calling them *ochlo-species*' (White, 1962: 79). Without further extensive and detailed field study of numerous populations of *B. owariensis*, recognition of subspecific taxa remained informal.

RELATIONS OF THE SPECIES OF *BRILLANTAISIA* 1: FORMULATION OF THE DATA MATRIX

Choice of outgroup

Multiple outgroups were chosen. Species were selected both from within the tribe Hygrophileae (*Hygrophila* species) and outside the tribe Hygrophileae. Within the tribe Hygrophileae, six species of *Hygrophila* were selected. These species represent the morphological and geographical variation of the genus, they are well delimited with no problems regarding species concept and they are represented by plenty of herbarium material at K and BM. Outside the tribe Hygrophileae, single species of the five genera considered most closely related to the Hygrophileae by Vollesen (pers. comm.) were included in the analysis.

Choice of characters

Stevens (1991), Wilkinson (1995) and Gift & Stevens (1997) all noted that individual scientists take very different approaches to character choice and character state delimitation and unfortunately, rarely explicitly state the criteria used at this stage of their research. Stevens (1984: 395) stated that 'the common meeting place of the systematist and morphologist is the analysis of similarity and its conversion into hypotheses of homology' and recently Pleijel (1995: 309) wrote that 'character coding represents the link between obser-

vation and analysis and greatly influences the results [of phylogeny reconstruction], but has nevertheless received little attention'. Thiele (1993: 275) described the method of converting description of morphology into comparative data for analysis as a filter that 'operates between the discovery of variation and the recording of that variation in the data matrix. Details of operation of the filter are often obscure...'. The main issues to be considered in coding morphological data for cladistic analysis are the coding of continuous versus discrete characters (e.g. Pimentel & Riggins, 1987; Cranston & Humphries, 1988; Chappill, 1989; Bateman et al., 1992; Gift & Stevens, 1997), the treatment of multistate versus binary data (compare Pimentel & Riggins, 1987; Pleijel, 1995; Wilkinson, 1995), ordered versus unordered characters (see Mickevich & Lipscomb, 1991: 127; Scotland, 1992c: 16; Quicke, 1993: 25 for illustrations of different character state transformation series), and missing entries in a data matrix (Doyle & Donoghue, 1986; Nixon & Davis, 1991; Platnick, 1991; Maddison, 1993).

In this study, 'ordinary character coding is based on the notion of character-state transformation series, in which states of the same character are seen as transformations of one another, and the whole assemblage of mutually transformable states forms a character' (de Pinna, 1996: 10). In this paper, the term binary refers only to presence/absence characters and not to two-state characters, for example 2 or 4 stamens. Multistate characters are consequently taken to be all characters with two or more states. This definition clarifies the difference between binary and two-state characters where the 0 may mean two completely different things: either 0 is the absence of character state 1 (binary), or 0 is the presence of a different character state homologous to 1 (two-state/multistate). Only discrete characters were selected for cladistic analysis. Continuously variable characters were excluded in this study because of subjectivity in coding character states (Pimentel & Riggins, 1987; Gift & Stevens, 1997) and because these data inflate tree length (Cranston & Humphries, 1988). All assumptions regarding the direction of transformation series were considered inappropriate prior to analysis (Hauser & Presch, 1991) and characters were treated as unordered throughout.

The data matrices

In preliminary analyses, discussed in Sidwell (1997), 48 characters were scored for 23 taxa forming a baseline data matrix from which all further analyses were derived. Missing data were present in 19/48 characters and in 19/23 taxa either because it was inapplicable to score a character for a particular taxon, or because a taxon was polymorphic for a particular character. In the analysis presented here, the baseline data matrix was transformed to remove both inapplicable and polymorphic missing data from the analyses. Three groups of characters were recoded to remove inapplicable missing data following Maddison (1993) and seven taxa, polymorphic for at least one character, were divided into monomorphic subunits following Nixon & Davis (1991). The 32 characters used in these analyses are presented in Table 1. The data matrix of 32 terminal units scored for the 32 characters is presented in Table 2.

RELATIONS OF THE SPECIES OF *BRILLANTAISIA* 2: ANALYSIS OF THE DATA MATRIX

Data were analysed using the mh*bb* command of HENNIG86 version 1.5 (Farris, 1988). Tree Gardener version 2.2 (Ramos, 1997) was used to edit matrices, run HENNIG86 via a windows shell and to

Table 1 List of 32 characters, numbered 0–31 to fit with conventions of HENNIG86 (Farris, 1989), scored for cladistic analysis of 32 taxa of Acanthaceae listed in Table 2.

No.	Character description
0.	Inhibition and/or innovation zones below synflorescence: absent (0), present (1)
1.	Leaf blade shape: broadly ovate to ovate 1:1-2 (0), linear-lanceolate (1)
2.	Leaf margin: entire or subentire (0), strongly rather irregularly toothed (1)
3.	Leaf pubescence: glabrous (0), pubescent (1)
4.	Petiole: absent (0), present unwinged (1), present entire or subentire wing (2), present clearly toothed wing (3)
5.	Proliferation zone: absent (0), present (1)
6.	Main florescence shape: spicate (0), paniculate (1)
7.	Enrichment zone of axillary/lateral inflorescences: absent (0), present (1)
8.	Bract shape: broadly ovate/ovate/linear (0), obovate/rounded (1)
9.	Bract base: not clasping rachis (0), clasping rachis (1)
10.	Bract pubescence: eglandular (0), glandular (1)
11.	Sepal length: equal/subequal (0), unequal (1)
12.	Sepal shape: linear (0), spatulate (1)
13.	Sepal fusion: free (0), fused (1)
14.	Sepal width: upper sepal slightly wider than the lower four (0), upper sepal highly developed, usually twice as wide as the lateral sepals (1)
15.	Corolla shape: not bilabiate (0), bilabiate hooded but not laterally compressed (1), bilabiate hooded and laterally compressed (2),
16.	Corolla hinge: absent (0), present (1)
17.	Upper corolla lip pubescence: subglabrous (0), glandular pubescent (1)
18.	Stiff trichomes on lower corolla lip: absent (0), present (1)
19.	Stamen arrangement: four fertile stamens (0), two posterior stamens with staminodes ca 1mm long (1), two posterior stamens with staminodes >2mm long (2), two anterior stamens with no staminodes
20.	Anther spur: absent (0), present (1)
21.	Number of colporate apertures in pollen: three (0), four (1)
22.	Colpus size: long (0), short/very short (1)
23.	Paired aperture position: equatorial (0), opposite pairs at uneven height (1)
24.	Atrium at pore: absent (0), present (1)
25.	Pollen shape: spheroidal (0), prolate or subprolate (1)
26.	Collumellae shape: not branched at base (0), branched at base (1)
27.	Ornamentation: single reticulum (0), double reticulum (1)
28.	Spines on pollen: absent (0), present (1)
29.	Style: not persistent in fruit (0), persistent in fruit (1)
30.	Number of ovules in the fruit (both locules): less than ten (0), greater than 10 (1)
31.	Fruit trichomes: absent (0), present (1)

view trees. CLADOS (Nixon, 1992) was used to look at character distribution on the HENNIG86 trees. Two types of character transformations were plotted onto the trees using CLADOS: either as unique occurrences (synapomorphies) in black or white or convergence or parallelism (homoplasy) in grey. The values of tree length, consistency index (CI) and retention index (RI) are provided. All characters are treated throughout as unweighted.

Results

The analysis produced 122 equally parsimonious trees, 87 steps long, CI=0.42 and RI=0.76. Tree 25/122 is presented in Figure 6 and the strict consensus of these trees is presented in Figure 7. Apart from a few collapsed nodes, the consensus tree (Fig. 7) is very similar to the tree given in Figure 6, and the major clades are the

same in both trees. Although the consensus tree (Fig. 7) is accepted as a working hypothesis of the phylogeny of *Brillantaisia*, the results are discussed here with reference to the characters shown on the tree in Figure 6. The results show that *Brillantaisia* and six species of *Hygrophila* both belong within a monophyletic group, the tribe Hygrophileae, based on a suite of pollen characters [21(1); 22(0); 23(1); 24(0); 25(0); 26(0) & 27(1)] and an entire to subentire leaf margin [2(0)] (this character reverses further up the tree [2(1)] in the species *B. kirungae*, *B. owariensis* and *B. vogeliana*). The outgroup to the *Brillantaisia*-*Hygrophila* clade is a group with non-bilabiate corollas [15(0)] containing the species *Eremomastax speciosa*, *Mellera lobulata* and *Mimulopsis solmsii*. The ((*Brillantaisia*-*Hygrophila*) (*Eremomastax* (*Mellera*-*Mimulopsis*))) clade is characterized by the presence of paniculate inflorescences [6(1)] and sepals which are free or fused only slightly at the base [13(0)].

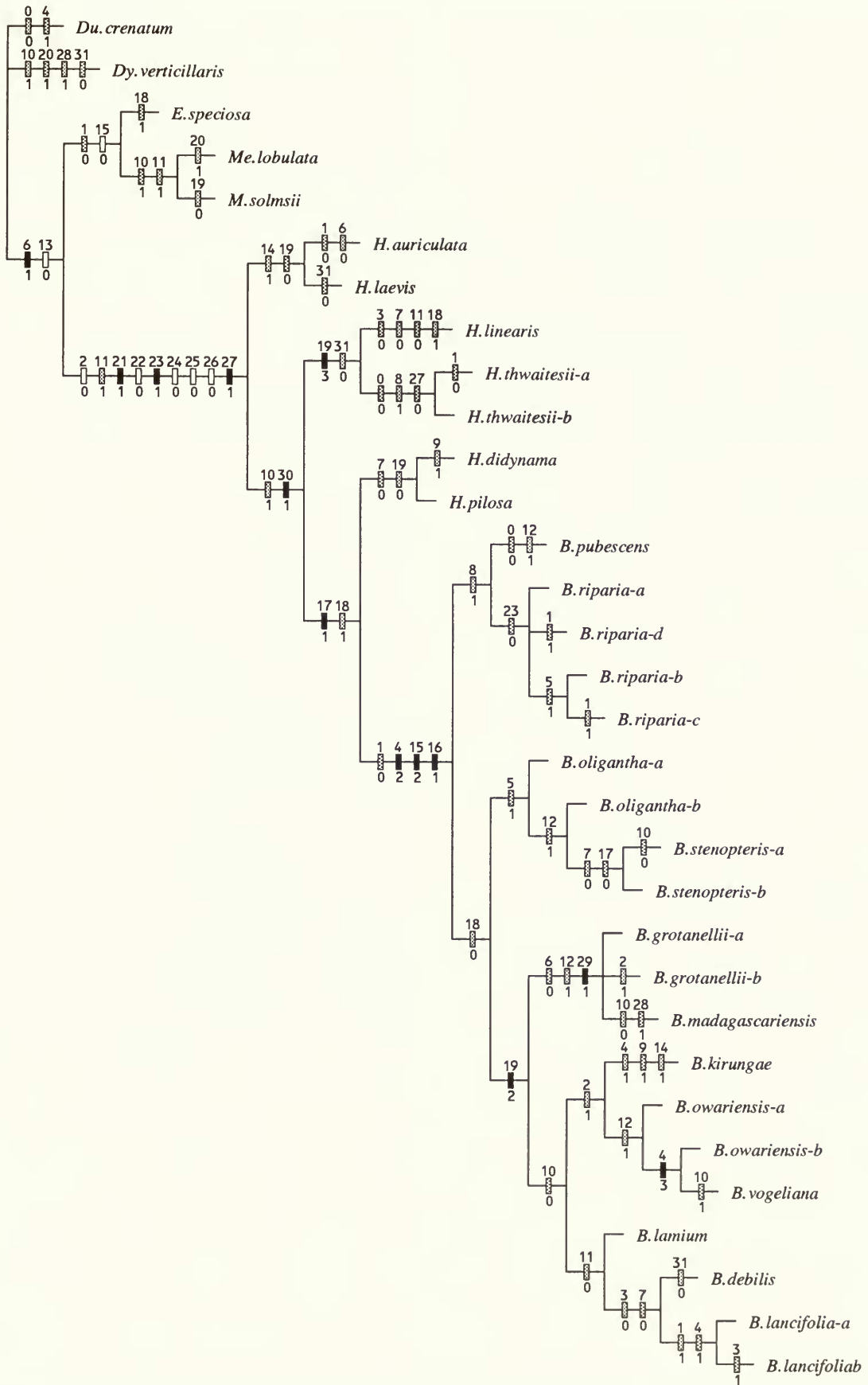
Table 2 Data matrix of 32 terminal units derived from recoding polymorphic missing data scored for the 32 morphological characters presented in Table 1.

Taxon	Character number						
	0-4	5-9	10-14	15-19	20-24	25-29	30/31
<i>Duosperma crenatum</i> (Lindau) P.G. Meyer	01111	0?1?0	00010	10001	00101	11000	01
<i>Dyschoriste verticillaris</i> C.B. Clarke	11110	00100	10010	100?1	10101	11?10	00
<i>Eremomastax speciosa</i> (Hochst) Cufod.	10110	01100	00000	00011	00101	11000	01
<i>Mellera lobulata</i> S. Moore	10110	01100	11000	00001	10101	11000	01
<i>Mimulopsis solmsii</i> Schweinf.	10110	01100	11000	00000	00101	11000	01
<i>Hygrophila auriculata</i> (Schumach.) Heine	10010	00100	01001	10000	01010	00100	01
<i>Hygrophila didynama</i> (Lindau) Heine	11010	01001	11000	10110	01010	00100	11
<i>Hygrophila laevis</i> Lindau	11010	01100	01001	100?0	01010	00100	?0
<i>Hygrophila linearis</i> Burkill	11000	01000	10000	10013	01010	00100	10
<i>Hygrophila pilosa</i> Burkill	11010	01000	11000	10110	01010	00100	11
<i>Hygrophila thwaitesii</i> (Benth.) Heine-a	00010	01110	11000	10003	01010	00000	10
<i>Hygrophila thwaitesii</i> (Benth.) Heine-b	01010	01110	11000	10003	01010	00000	10
<i>Brillantaisia debilis</i>	10002	01000	00000	21102	01010	00100	10
<i>Brillantaisia grottanellii</i> -a	10012	00100	11100	21102	01010	00101	11
<i>Brillantaisia grottanellii</i> -b	10212	00100	11100	21102	01010	00101	11
<i>Brillantaisia lamium</i> .	10012	01100	00000	21102	01010	00100	11
<i>Brillantaisia lancifolia</i> -a	11001	01000	00000	21102	01010	00100	11
<i>Brillantaisia lancifolia</i> -b	11011	01000	00000	21102	01010	00100	11
<i>Brillantaisia madagascariensis</i>	10012	00100	01100	21102	01010	00111	11
<i>Brillantaisia oligantha</i> -a	10012	11100	11000	21101	01010	00100	11
<i>Brillantaisia oligantha</i> -b	10112	01100	01100	21102	01010	00100	11
<i>Brillantaisia owariensis</i> -a	10112	01100	01100	21102	01010	00100	11
<i>Brillantaisia owariensis</i> -b	10113	01100	01100	21102	01010	00100	11
<i>Brillantaisia pubescens</i> .	00012	01110	11100	21111	01010	00100	11
<i>Brillantaisia riparia</i> -a	10012	01110	11000	21111	01000	00100	11
<i>Brillantaisia riparia</i> -b	10012	11110	11000	21111	01000	00100	11
<i>Brillantaisia riparia</i> -c	11012	11110	11000	21111	01000	00100	11
<i>Brillantaisia riparia</i> -d	11012	01110	11000	21111	01000	00100	11
<i>Brillantaisia stenopteris</i> -a	10012	11000	01100	21001	01010	00100	11
<i>Brillantaisia stenopteris</i> -b	10012	11000	11100	21001	01010	00100	11
<i>Brillantaisia kirungae</i>	10111	01101	01001	21102	01010	00100	11
<i>Brillantaisia vogeliana</i> .	10113	01100	11100	21102	01010	00100	11

Duosperma crenatum and *Dyschoriste verticillaris* form an unresolved outgroup to all other species in this analysis. Within the *Brillantaisia*-*Hygrophila* clade, the twelve species of *Brillantaisia* form a monophyletic genus based on a laterally compressed upper corolla lip [16(1)], a membranous hinge at the apex of the corolla tube [15(2)] and a winged petiole with an entire or subentire margin [4(2)]. Within *Brillantaisia*, a clade containing eight species is delimited on the presence of staminodes greater than 2 mm long [19(2)]. The other four species within the genus all have minute staminodes and form a partially unresolved outgroup to that clade. Section *Stenanthium* of Lindau, recognized by him as consisting of all species of *Brillantaisia* with spicate inflorescences (*B. grottanellii* and *B. madagascariensis*) is monophyletic in this analysis based on the persistence of the style in fruit [29(1)], a character which maybe an artifact of the maturity of specimens

examined for those species and requires reconsideration. Section *Stenanthium* of Lindau containing all other species of *Brillantaisia* is paraphyletic. Subgeneric taxa are not formally recognized in this account. The six species selected to represent *Hygrophila* form successive pairs of sister taxa to *Brillantaisia*. However, in this analysis, *Hygrophila* is paraphyletic and requires further study, including a more comprehensive cladistic analysis, before the precise sister group to *Brillantaisia* can be identified. *Hygrophila* is necessarily accepted as a paraphyletic genus for nomenclatural convenience, but it should be recognized as a diverse group, in need of revision, and is best conceived as comprising all members of the tribe Hygrophileae that do not belong within *Brillantaisia*. Within the constraints of time and the Linnaean hierarchy, acceptance of well known groups which are paraphyletic is inevitable.

Fig. 6 One of 122 equally parsimonious trees (tree 25/122) produced from analysis of the data matrix in Table 1. Synapomorphic characters are shown by the black and white bars and homoplasious characters by the grey bars. Character numbers are given above each bar and the state of that character is given below each bar.



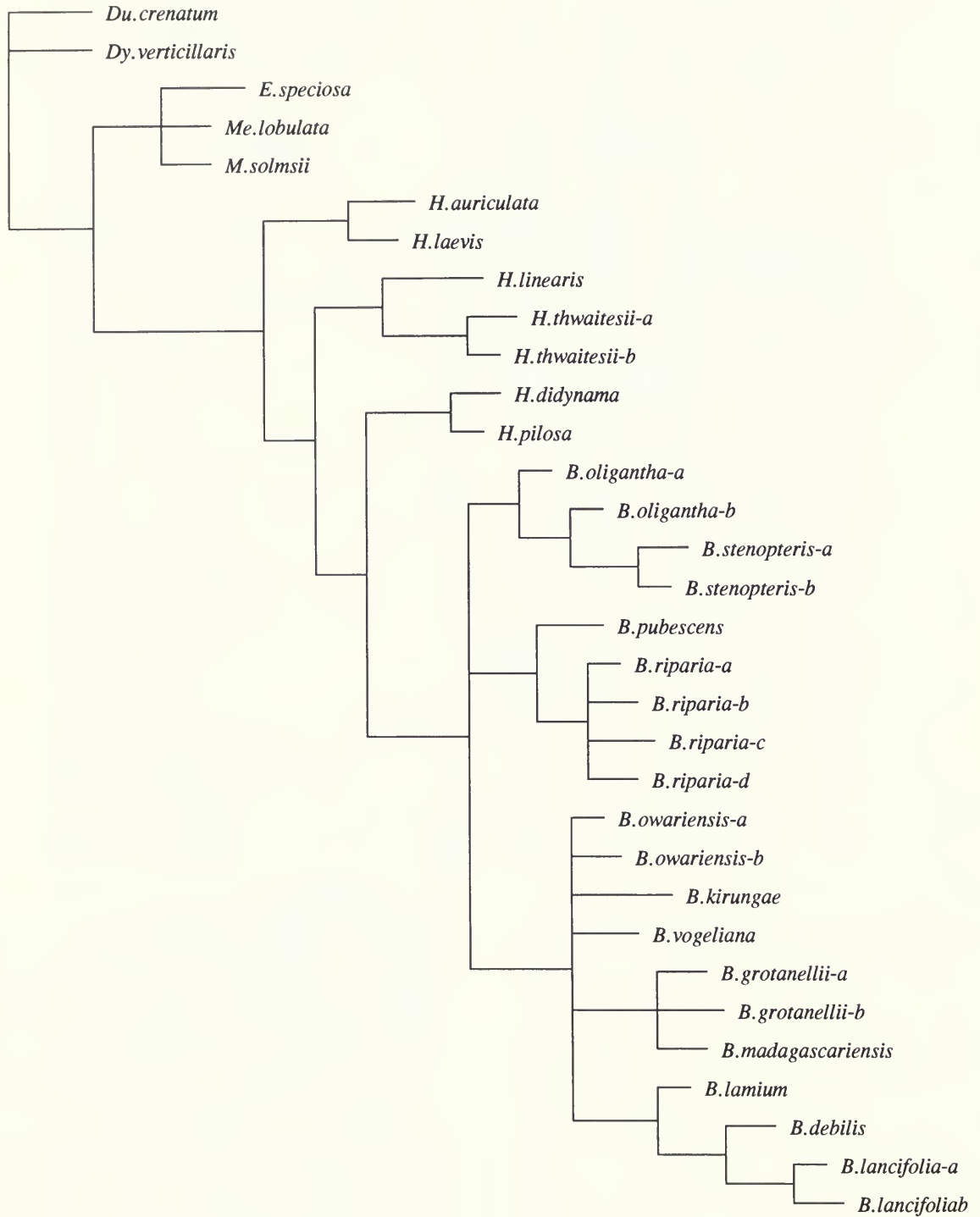


Fig. 7 Strict consensus of 122 trees produced from analysis of the data matrix in Table 1.

TAXONOMIC ACCOUNT

Brillantaisia P. Beauv., *Flore d'Oware* 2: 67. t. 100, fig. 2 (1818); Burkill in *Fl. trop. afr.* 5: 37 (1899); Durand & Durand, *Syll. fl. congol.*: 416–418 (1909); Chevalier, *Explor. bot. Afrique occ. franç.* 1: 493 (1920); Robyns, *Fl. parc nat. Albert* (1947); Heine in *Fl. W. trop. Afr.* 2nd ed., 2: 405 (1963); Heine in *Fl. Gabon* 13: 28 (1966); Benoist, *Fl. Madag. fam.* 182: 28 (1967); Agnew, *Upl. Kenya wild fls.* 583 (1974); Troupin, *Fl. pl. lign. Rwanda*: 84 (1982); Champluvier in *Fl. Rwanda* 3: 444 (1985). Type species: *Brillantaisia owariensis* P. Beauv., *Flore d'Oware* 2: 68, t. 100: fig. 2 (1818).

Belantheria Nees in DC., *Prodr.* 11: 96 (1847). Type species: *Belantheria belvisiana* Nees in DC., *Prodr.* 11: 96 (1847).

Leucoraphis Nees in DC., *Prodr.* 11: 97 (1847). Type species: *Leucoraphis vogeliana* Nees in DC., *Prodr.* 11: 97 (1847).

Ruellia Baillon in *Bull. Mens. Soc. Linn. Paris* 2: 852 (1890); Baillon, *Hist. pl.* 10: 427 (1891); Lindau in *Nat. Pflanzenfam.* 4(3b): 307 (1895). Type species: *Ruellia grevei* Baillon in *Bull. Mens. Soc. Linn. Paris* 2: 852 (1890).

Erect to prostrate herbs to erect, sturdy shrubs. *Stems* square, usually swollen at the nodes, glabrous to densely pubescent; cystoliths longitudinal, narrowing towards one end. *Leaves* opposite, decussate, petiolate, broadly ovate to ovate, occasionally elliptic or linear-lanceolate; leaf base cordate or truncate to cuneate; apex acute or acuminate; margin entire to irregularly toothed; glabrous to pubescent above and below; indumentum of multicellular, eglandular trichomes, evenly pilose to dense and villose above, mainly on midrib and primary lateral veins below; cystoliths usually visible, with a hand lens, above and below over entire leaf surface. *Petiole* usually winged, lamina decurrent in top half of petiole, though occasionally broadly winged to base; petiole wing margin entire, occasionally toothed towards apex. *Inflorescence* a variously modified dichasium forming either a terminal thyrse and/or lateral axillary thyrse with vegetative growth occasionally continuing above flowering axes; dichasial branching usually lax, becoming monochasial towards base of inflorescence, occasionally contracted forming spike with flowers appearing in verticillasters. *Bracts* on main inflorescence axis ovate to broadly ovate, foliaceous, equal in size to the uppermost leaves at base of inflorescence, becoming smaller towards the apex of the inflorescence; *bractlets* on lateral inflorescence branches linear to obovate. *Calyx* with five equal or unequal, linear to spatulate sepals, dorsal sepal longer and usually broader than the four lateral sepals; usually hirsute, with glandular and eglandular trichomes. *Corolla* two-lipped, purple, magenta, blue or violet, occasionally white; corolla tube cylindrical, often paler than corolla lobes, with two brown-yellow markings in throat; upper lip hooded, laterally compressed, two-lobed at apex, often glandular pubescent on outer surface; lower lip broad, ridged and bullate above, reflexed at edges, three-lobed at apex, occasionally with stiff trichomes on adaxial surface, two membranous lateral pouches at base of lower lip form a hinge with the apex of the corolla tube. *Androecium* with two posterior stamens fertile; filaments white, flattened, often sparsely pubescent towards the base; anthers sagittate, dorsifixed; two anterior stamens reduced to slender staminodes, often with membranous vestigial anther at apex, occasionally minute or absent. *Gynoecium* with slender, linear style, often sparsely pubescent towards base; stigma a single flattened lobe at the end of the style, second, lower lobe reduced to minute tooth; ovary two-locular on annular disc, usually pubescent, placentation axial; ovules numerous. *Fruit* a linear, convex, two-valved capsule, pointed at apex with deep longi-

tudinal groove down centre of each valve, green with red apex when immature, brown to black when dry, glabrous or glandular and/or eglandular pubescent, elastically dehiscent. *Seeds* rounded to slightly kidney shaped, flattened, each held on a hardened, hook-shaped retinacula, covered with adpressed trichomes which are hygroscopic and expand rapidly, producing mucous when wet.

DISTRIBUTION. Throughout tropical Africa with two species extending to Madagascar.

HABITAT. The distribution of *Brillantaisia* species is centred in the Guineo-Congolian rain forests with species also occurring in montane rain forests and woodland throughout Africa. Plants of *Brillantaisia* are often found in mesic sites or rooted in water and when in drier savannah type vegetation only occur in shady, wetter places. In West Africa *Brillantaisia* is commonly found in disturbed areas (e.g. roadsides, plantations, farmland).

Brillantaisia is a genus of 12 species several of which are widespread and tend to be very variable morphologically, and is most diverse in the Guineo-congolian forests. Many species have previously been described in the genus based on local variation which has been shown to be continuous by extensive study of specimens. The variation within each species is discussed in detail after each description. A full list of specimens studied is provided in Sidwell (1997) and a constantly updated list is available from the author.

Key to fertile specimens of *Brillantaisia*

1. Inflorescence a contracted thyrse with short peduncles, forming a spike; flowers/fruit in verticillasters 2
 Inflorescence a lax thyrse with elongated, clearly visible peduncles 3
2. Bracts with glandular and eglandular trichomes, linear-ovate; style often pubescent towards apex 11. **B. grottanellii**
 Bracts lacking glandular trichomes, ovate to broadly ovate; style pubescent only at base 12. **B. madagascariensis**
3. Bractlets obovate-rounded, shortly petiolate; corolla lips less than twice the length of the corolla tube; sepals spatulate; flowers with stiff, unicellular trichomes on inner surface of lower lobe 4
 bractlets linear; corolla lips more than twice the length of the corolla tube; sepals linear or spatulate; flowers lacking unicellular trichomes on inner surface of lower lobe 5
4. Flowers small, 12–25 mm long, inflorescence highly branched; leaves 1.25–1.8 times longer than wide 1. **B. pubescens**
 Flowers large, 30–40 mm long; inflorescence branched 3–4 times; leaves 1.9–3.0 times longer than wide 2. **B. riparia**
5. Leaves lanceolate to elliptic, occasionally ovate, entire or barely crenate; inflorescence narrow terminal thyrse branching 1–2 times 9. **B. lancifolia**
 Leaves ovate to broadly ovate, entire or clearly toothed; inflorescence lax, open, terminal or lateral thyrse branching 2–many times 6
6. Fruit glabrous or with a few erect trichomes at the apex; leaves entire or subentire 7
 Fruit pubescent; leaves toothed, or if leaves entire to subentire, inflorescences slender, lateral, thyrse with apex usually reverting to vegetative growth 8
7. Leaves pubescent particularly towards petiole; fruit 22–30 × 2–5 mm, with 14–16 seeds per locule 8. **B. lamium**
 Leaves usually glabrous; fruit 18–22 × 1–2 mm, with 18–28 seeds per locule 10. **B. debilis**

8. Fruit with 8–10 very rarely to 16 seeds per locule; woody shrub or small tree, leaves often drying black 6. **B. kirungae**
Fruit always with more than 12 seeds per locule; herb to 2 m tall, not drying black 9
9. Flowers 15–25 mm long (rarely to 35 mm); fruit with 20–24 seeds per locule; leaves thin, rather papery when dry, often toothed at the top of the petiole wing 7. **B. vogeliana**
Flowers 30–45(–50) mm long; fruit with 12–20 seeds per locule; leaves not thin and papery when dry, petiole wing usually entire 10
10. Lower corolla lip with clearly visible multicellular trichomes on upper surface 3. **B. oligantha**
Lower corolla lip glabrous 11
11. Leaf margin subentire or with small serrations; petiole wing tapering gradually to base of petiole; lower corolla lip strongly reflexed, centre of lower lip bent up to 90° 4. **B. stenopteris**
Leaf margin usually strongly toothed; petiole wing tapering gradually to broad and toothed; lower corolla lip not strongly reflexed 5. **B. owariensis**

1. **Brillantaisia pubescens** T. Anderson ex Oliv. in *Trans. Linn. Soc. London* **29**: 125 (1875); Burkill in *Fl. trop. afr.* **5**: 38 (1899); Durand & Durand, *Syll. fl. congol.*: 417 (1909); De Wild., *Contr. Fl. Katanga* **1**: 143 (1913); Benoist in *Cat. pl. madag.* **13** (1939); Vollesen in *Opera Bot.* **59**: 79 (1980); Vollesen & Brummitt in *Kew Bull.* **36**: 571 (1981). Type: Tanzania, Khutu, Kirengwe, Grant s.n. (K!-holotype).

Fig. 8. Map in Vollesen & Brummitt (1981: 571).

Brillantaisia rutenbergiana Vatke in *Abh. Naturwiss. Vereine, Bremen* **9**: 131 (1885); Palacky, *Cat. pl. madag.* **3**: 57 (1907). Type: Madagascar, Andranovaka, Rutenberg s.n. (P-holotype).

Ruellia grevei Baillon in *Bull. Mens. Soc. Linn. Paris* **2**: 852 (1890); Baillon, *Hist. pl.* **10**: 427 (1891); Lindau in *Nat. Pflanzenfam.* **4**(3b): 307 (1895). Type: Madagascar, Greve 26 (P!-holotype; P!-isotype).

Brillantaisia anomala Lindau in *Pflanzenw. Ost-afri.* **C**: 366 (1895); Lindau in *Bot. Jahrb. Syst.* **24**: 312–313 (1898); Lindau in *Nat. Pflanzenfam.* **4**(3b): 296 (1895). Type: Mozambique, Villa Gouveia, de Carvalho s.n. (COI-holotype).

B. pubescens var. *rutenbergiana* (Vatke) Benoist in *Cat. pl. madag.* **13** (1939).

Hygrophila pubescens (T. Anderson ex Oliv.) Benoist in *Fl. Madag. fam.* **182** **1**: 36 (1967) non Nees (1847).

Icones: Anderson in *Trans. Linn. Soc. London* **29**: pl. 125 pro parte (1875); Benoist in *Fl. Madag. fam.* **182** **1**: fig. IV 14–18 (1967).

Straggling annual, highly branched, aromatic herb, (0.3–)0.45–1 m tall, smelling minty or balsamic. *Stems* 2–5(–14) mm in diameter, covered in short glandular trichomes and longer fine, white eglandular trichomes. *Leaves* broadly ovate to ovate 50–110 × 85–160 mm, often caducous; leaf base cuneate to shortly attenuate, occasionally truncate; apex acute; margin entire, occasionally slightly crenate; indumentum of silky, eglandular trichomes above and below; lateral veins 7–9(–13) each side of midrib; petiole to 75 mm long, winged towards lamina, wing narrow, decurrent on petiole in upper 1/2–1/2. *Inflorescence* highly branched open thyrse with lateral inflorescences to base of stem, branches slender, rachis indumentum irregularly glandular-pubescent with longer eglandular trichomes. *Bracts* obovate to elliptic, to 35 × 45 mm, petiolate, irregular glandular pubescent on both surfaces; bractlets obovate-rounded, to 5 × 8 mm, persistent. *Sepals* unequal, spatulate, larger upper sepal 12–14 × 0.5 mm, 1.5–2 mm wide at broadened apex, smaller lateral sepals 8–10(–13) × < 0.5 mm, pubescence of slender eglandular trichomes with shorter glandular trichomes, denser towards spatulate apex. *Corolla* purple to pale purple/pink occasionally with white upper lip, tube 5–10 mm long; upper lip 8–13(–15) mm long, pubescent externally; lower lip 7–12(–15) mm; trichomes on lower lip white, purple at apex; apical lobes 1 × 1 mm, central lobe smaller. *Androecium* with filaments 6–8 mm long; anthers 1–2.5 mm long; staminodes minute < 0.5 mm long or absent, glabrous. *Gynoecium* with style 8–9 mm long; stigma 1 mm long; ovary 2–3 mm long, glandular pubescent. *Capsule* 10–15 × 2–2.5 mm with 8–16 seeds per locule, yellow brown when dried, sparsely glandular pubescent with longer eglandular trichomes towards the apex.

DISTRIBUTION. East and Central Africa, Malawi, Zambia, Zimbabwe, Mozambique and Tanzania, west to Zaire, Madagascar.

HABITAT. Sandy dry places, river beds, shade on forest floor or in savannah woodlands under, for example, *Adansonia digitata* and *Faidherbia albida* trees, or with *Acacia*, *Albizia*, *Parkia*, *Lepisanthia* and *Terminalia* (Abdallah & Vollesen 95/176 K). Locally common; 0–1000 m.

SELECTED COLLECTIONS

DEMOCRATIC REPUBLIC OF THE CONGO: Upemba National Park, Kaswabilenga, 17 June 1948, 700 m, de Witte 03986 (BR, K). TANZANIA: Lindi, 11 September 1934, Schlieben 5323 (G, H, LISC, M, MO, PRE, S, US, Z); 2 km NW of Kingupira, 5 June 1975, Vollesen 2392 (C); 6 km along Kisiwani-Mnazi road, 800 m, 7 May 1995, Abdallah & Vollesen 95/176 (K). MOZAMBIQUE: Maringua, Dabi river, 25 June 1950, Chase 2547 (BM). MALAWI: Salima, Chipoka near Ilala Quarry, 25 May 1972, Salubeni 1803 (MO, SRGH); Chimpakati village, Mlunguzi River, 27 June 1987, Usi & Kaunda 606 (MAL). ZAMBIA: Petuake district, 5 September 1947, Greenway & Brenan 8044 (PRE); NW of Mwern-na-ntipa, 7 August 1962, Tyres 339 (SRGH). ZIMBABWE: Binga district, September 1955, Davies 1426 (MO, SRGH); Urungwe district, 20 September 1981, Pope 1987 (MO, SRGH). MADAGASCAR: Perrier 9416 (P); Madirobe, July 1912, Kaudern s.n. (S).

Table 3 Four characters that differ between plants of *Brillantaisia pubescens* and *B. riparia*.

Character	<i>B. pubescens</i>	<i>B. riparia</i>
Inflorescence type	very highly branched	branched 3–4 times
Corolla length	to 25 mm	30–40 mm long
Hinge at apex of corolla tube	not well developed	well developed
Leaf shape	ovate	elliptic



Fig. 8 *Brillantaisia pubescens* T. Anderson ex Oliv. A. Habit $\times 0.7$; B. Lower leaf $\times 0.7$; C. Bract and bractlets $\times 1$; D. Gynoecium $\times 3$; E. Corolla dissection showing androecium $\times 3$; F. Capsule $\times 4$.

Brillantaisia pubescens is one of the more distinctive species in the genus. The highly branched inflorescence, small flowers and rounded persistent bracts are not found elsewhere in *Brillantaisia*. *Brillantaisia pubescens* sensu lato was split into two subspecies by Vollesen & Brummitt (1981) on the basis of flower size. I consider the large flowered plants to be a different species (*B. riparia*) and treat *B. pubescens* s.s. as including only those plants with smaller flowers. Two specimens of *B. pubescens* have slightly larger flowers than most (Tinley 2639, SRGH; Thera & Kaunda 313, PRE); however, the leaf shape and venation are that of *B. pubescens* and this variation does not blur the boundary between *B. pubescens* and *B. riparia*. The original illustration of the small flowered *B. pubescens* by Fitch (Anderson 1875: pl. 125) almost certainly contributed to confusion over species delimitation as the type specimen was represented as having many more, larger flowers than it actually has. It appears that large flowered specimens of *B. riparia* have been identified as *B. pubescens* by reference to the illustration. There are several characters by which plants of the two taxa can be clearly distinguished (Table 3).

2. ***Brillantaisia riparia*** (Vollesen & Brummitt) Sidwell, **comb. nov.** Type: Malawi, 13 miles N. of Kasungu, Dwangwa River, Pawek 3908 (K!-holotype).

Fig. 9. Map in Vollesen & Brummitt (1981: 571).

Brillantaisia pubescens var. *riparia* Vollesen & Brummitt in *Kew Bull.* **36**: 571 (1981); Vollesen in *Opera Bot.* **59**: 79 (1980).

Icon: Anderson in *Trans. Linn. Soc. London* **29**: pl. 125 pro parte (1875).

Annual viscid-pubescent, aromatic, rather woody herbs to 0.5–1 m tall. *Stems* erect or ascending; pilose with eglandular and glandular trichomes. *Leaves* oblong, elliptic to ovate 20–25(–52) × 39–59(–95) mm, often fallen below; upper most leaves of main axis oblong, 5–8 × 10–15 mm; base gradually tapering, cuneate; apex acute, rounded at tip; margin entire to slightly crenate; glabrous to pilose; lateral veins 4–9(–11) each side of midrib; petiole 14–22 mm long, lamina decurrent on petiole forming very narrow wing sometimes to base. *Inflorescence* leafy-bracteate terminal thyrse, with lower lateral panicles, occasionally with vegetative growth continuing at apex; rachis covered in short simple trichomes with longer fine, non glandular and stalked glandular trichomes. *Bracts* as leaves; bractlets elliptic-obovate, rounded at apex, margin entire, glandular trichomes and slender white trichomes above and below. *Sepals* unequal, larger upper sepal linear-spathulate, 14–18 × 1 mm; smaller lateral sepals spatulate, 9–14 × 0.5–1 mm. *Corolla* purple to blue-purple; corolla tube 13–15 × 2 mm; upper lip 20–25 mm long, glabrous; lower lip

20–25 mm long, glabrous below, with straight erect stiff trichomes on centre of inner surface, trichomes white with a dark purple-black tip; apical lobes 2 × 2–3 mm, triangular, rounded to blunt or notched at apex. *Androecium* with filaments (10–)20–22 mm long; anthers 4–5 mm long; staminodes 3–4 mm long, pale, translucent, difficult to see with the naked eye, broadened slightly at apex sometimes to curved vestigial anther. *Gynoeceum* with style to 30 mm long, stiff upward pointing trichomes towards base; stigma 2 mm long; ovary 3 mm long glandular pubescent. *Capsule* 14–19 × 2 mm with 8–12 seeds per locule, light brown, covered with simple short trichomes and longer, glandular trichomes.

DISTRIBUTION. Mozambique and Malawi.

HABITAT. Damp, shady places; 1000 m.

SELECTED COLLECTIONS

MOZAMBIQUE: Vila Cabral, 8 September 1942, *Mendonça* 680 (LISC); Nampula, 3 October 1942, *Mendonça* 1219 (LISC); between Namapa and Chiure, 19 August 1948, *Barbosa* 1812 (LISC); Niassa, Vila Cabral, Meponda, 9 September 1958, *Monteiro* 46 (LISC). MALAWI: Kasungu, 27 August 1946, *Brass* 17442 (BM, MO, NY, SRGH, US); Machinga, 19 October 1979, *Banda & Salubeni* 1571 (MO, SRGH); Liwawazi river, 3 September 1986, *Kaunda & Usi* 429 (MAL); Liwonde, 9 September 1988, *Banda & Kaunda* 3452 (MO).

Brillantaisia riparia was considered a variety of *B. pubescens* by Vollesen & Brummitt (1981). Due to the difference in flower size and shape, leaf shape, leaf venation and inflorescence structure, I consider *B. riparia* a separate species from *B. pubescens*. The two species are clearly very closely related yet are easily distinguished in the field. Brummitt (pers. comm.) noted that *B. riparia* should be compared with *B. oligantha*. *Brillantaisia riparia* and *B. oligantha* are superficially similar, both having lateral inflorescences, trichomes on the lower lip of the corolla and flowers of roughly equal size. However, there are several differences in gross morphology (Table 4) that clearly separate the two.

3. ***Brillantaisia oligantha*** Milne-Redhead in *Mem. New York Bot. Gard.* **9**: 20–21 (1954); Binns, *Check List Herb. Fl. Malawi*: 12 (1968). Type: Malawi, Nchisi Mountain, 30 January 1946, *Brass* 17042 (K!-holotype; BM!, MO!-isotypes).

Fig. 10. Map 1.

Viscid herb 0.3–1.8 m tall. *Stems* 2–2.5 mm across, slightly winged on angles of stem, pubescent, with straggling eglandular and shorter multicellular glandular trichomes. *Leaves* ovate to broadly ovate, 36–65(–130) × 87–160(–210) mm; leaf base cuneate to attenuate; apex acuminate; margin subentire to shallowly crenate or dentate; subglabrous to roughly pubescent; 7–10(–16) lateral veins each side

Table 4 Four characters that differ between plants of *Brillantaisia riparia* and *B. oligantha*.

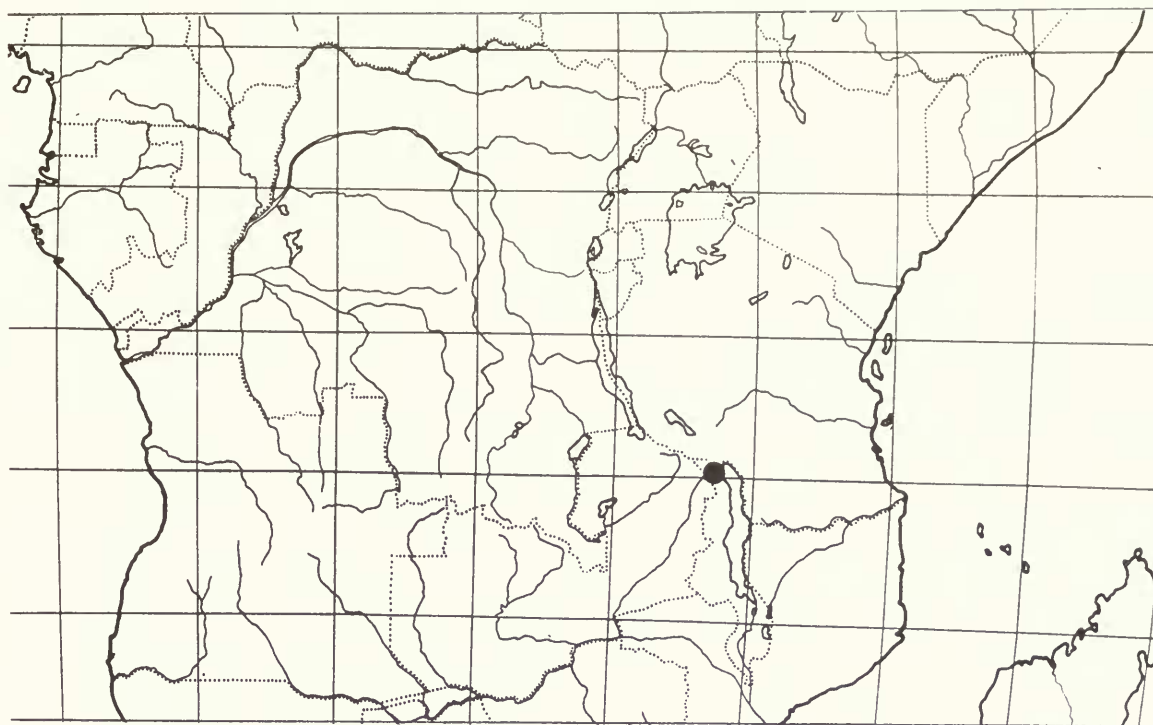
Character	<i>B. riparia</i>	<i>B. oligantha</i>
Inflorescence branching	stout, straight	slender, curving
Corolla tube	straight, long, narrow	inflated, short, broad,
Lower corolla lip trichomes	straight, single celled	multicellular
Lower corolla lip shape	gibbous, not strongly reflexed	strongly reflexed



Fig. 9 *Brillantaisia riparia* (Vollesen & Brummitt) Sidwell. A. Habit $\times 0.7$; B. Corolla dissection showing androecium $\times 2$; C. Capsule $\times 3.2$; D. Gynoeceum $\times 2$; E. Bract and bractlets $\times 1$.



Fig. 10 *Brillantaisia oligantha* Milne-Redhead. A. Habit $\times 0.7$; B. Corolla dissection showing androecium $\times 2.5$; C. Capsule $\times 1.8$; D. Gynoecium and calyx $\times 2.5$; E. Bract and bractlets $\times 3$.



Map 1 The distribution of *Brillantaisia oligantha* Milne-Redhead.

of midrib; petiole (15–)40–70(–120) mm long, lamina decurrent on petiole forming a slender wing almost to the base of the petiole. *Inflorescence* lateral few flowered thyrses to 45–75 mm long, branches very slender, branching 3–4 times, rachis pubescent. *Bracts* as leaves; bractlets narrowly obovate (0.3–)1.5–4 × (0.8–)2–9 mm, glandular pubescent above and below. *Sepals* unequal; linear to spatulate, larger upper sepal 6–10 × 1 mm, smaller lateral sepals 5–9 × 0.5 mm, pubescent. *Corolla* deep blue to purple, sometimes tinged brown on the upper lip, corolla tube 3 × 7.5 mm; upper lip 13–17 mm long, sparsely pubescent outside; lower lip 14–18 mm long, strongly reflexed with lateral fold down centre and deep hinge at base, multicellular trichomes on inner surface; apical lobes to 2.5 × 3 mm. *Androecium* with filaments 10–15 mm long, pubescent at base; anthers 1–4 mm long; staminodes 1 mm long with small vestigial anther. *Gynoecium* with style 1–1.5 mm long, pubescent along the entire length; stigma 20–25 mm long; ovary 3 × 1 mm, covered in short glandular trichomes. *Capsule* 20–27 × 1–2 mm with 10–12 seeds per locule, very sparse, short, glandular trichomes.

DISTRIBUTION. Restricted to the Nchisi and Mughese mountain ranges in Malawi.

HABITAT. Shady places in wet forest, or in dry evergreen or semi-evergreen forest, also along roadsides in these areas. Locally common; 1000–1400 m.

SELECTED COLLECTIONS

MALAWI: Nchisi Mountain, 29 July 1946, *Brass* 17021 (NY); 30 July 1946, *Brass* 17042 (BM, K, MO); 10 July 1960, *Chapman* 827 (BM); 1 September 1970, *Salubeni* 1485 (SRGH); *Salubeni* 1487 (MAL, PRE, SRGH); Chitipa district, Mughese, 12 September 1977, *Phillips* 2836 (MO); *Pawek* 12984 (K, LISC, MAL, MHU, MO, SRGH).

Brillantaisia oligantha is an easily distinguished species, with lat-

eral axillary inflorescences only. The lower corolla lip is more strongly reflexed in *B. oligantha* than in other species of the genus and has multicellular trichomes on the adaxial surface. Previously thought to be restricted to the Nchisi mountains of Malawi, collections from Mughese in Malawi are clearly the same species. *Brillantaisia oligantha* can appear morphologically similar to *B. riparia*, both species having entire leaves and fine white silky trichomes on vegetative parts, however, *B. oligantha* has a much shorter, broader corolla tube, a more hooded upper lip, and a more slender, less branched inflorescence. This species is also closely related to *B. stenopteris* Sidwell, sp. nov. from Tanzania. However, the new species has larger flowers, lacks any trichomes on the lower lip of the corolla and is found in a different habitat to *B. oligantha*.

4. *Brillantaisia stenopteris* Sidwell, sp. nov. Type: Tanzania, Morogoro region, Kombola, 8 July, 1933, *Schlieben* 4068 (LISC!-holotype, MO!, PRE!-isotypes)

Fig. 11. Map 2.

Herba perennis usque ad 2 m alta. Folia lamina ovata vel latiovata 25–144 mm longa, 40–220 mm lata, apice acuminata, basi cuneata, margine obscure serrata, lamina 11–16 venatus, petiolo breviter decurrense; petiolo 15–90 mm longo. Inflorescentia ad 20 cm longa, cymosa, terminalis, interdum vegetativus ad apice. Corolla 24–30 mm longa, tubus circiter 8–9 mm longus; labium posticum 18–22 mm longum; labium anticum 17–23 mm longum, glabrum. Fructus incognitus. Species nova affinis *Brillantaisia oligantha* Milne-Redh. sed floribus majoribus et labium anticum sine pilis longis septatis differt.

Herbs to 2 m tall. *Stems* erect, 2 mm in diameter, pubescent, trichomes white, eglandular with shorter glandular trichomes. *Leaves* ovate to broadly ovate 25–140 × 40–220 mm; leaf base cuneate; apex

acuminate; margin serrate, occasionally subentire; adaxial surface subglabrous to roughly pubescent, abaxial surface with fine non glandular trichomes; 11–16 lateral veins on each side of the midrib; petiole 15–90 mm long, lamina decurrent on the petiole forming a narrow wing, often to the base of the petiole. *Inflorescence* open panicle, sometimes becoming vegetative at the apex, to (4–)7–20 cm long; lateral branches slender, few flowered. *Bracts* as leaves or ovate, sessile; bractlets ovate-linear 7–12 × 1–3 mm. *Calyx* unequal, sepals slightly spatulate, larger upper sepal 10–12 × 1–2 mm, smaller lateral sepals 8–10 × 1 mm; covered in long non glandular and short glandular trichomes. *Corolla* purple, corolla tube 8–10 × 3 mm, upper lip to 18–22 mm long, glandular pubescent outside; lower lip 17–23 mm long, glabrous on inner surface. *Androecium* with filaments 25 mm long; anthers 4 mm long; staminodes 1 mm long, minute, lacking vestigial anther. *Gynoecium* with style 30 mm long; stigma 4 mm long; ovary 6 mm long, densely pubescent. *Capsule* not known.

DISTRIBUTION. Restricted to the Morogoro region of Tanzania.

HABITAT. Rain forest; 1000 m.

COLLECTIONS EXAMINED

TANZANIA. Morogoro region, Kombola, 8 July 1933 *Schlieben* 4068 (LISC, MO, PRE); Kilosa district, 13 November 1987, *Poçs* et al. 8722 (UPS).

Brillantaisia stenopteris is very closely related to *B. oligantha* from the Nchisi and Mughese mountains in Malawi. The two species have similar ovate, cuneate leaves with a long slender petiole wing. However, they can be easily distinguished due to the larger flowers and absence of trichomes on the inner surface of the lower corolla lip of *B. stenopteris*. The corolla tube of *B. stenopteris* is longer and thinner than that of *B. oligantha*, resembling the corolla tube of *B. riparia*, which is also closely related to *B. stenopteris*.

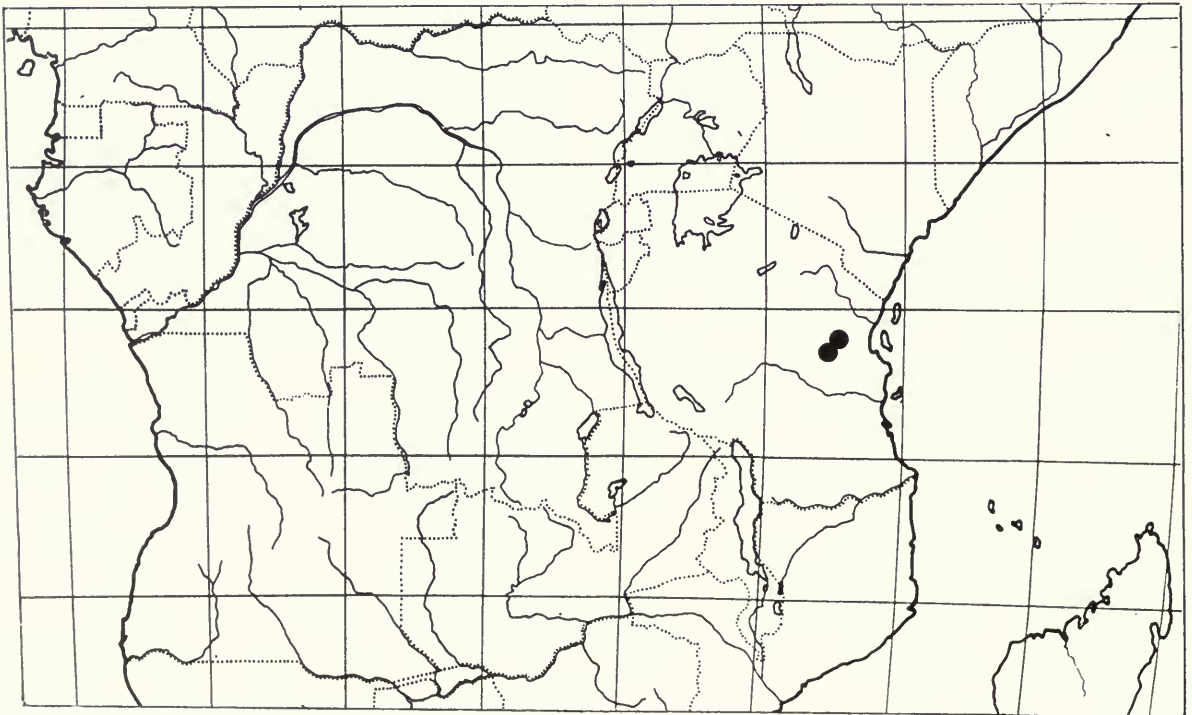
5. *Brillantaisia owariensis* P. Beauv., *Flore d'Oware* 2: 68 (1818); Bentham in *Niger Fl.*: 477 (1849); Hooker in *Bot. Mag.*: 79: t. 4717 (1853); Durand & Schinz, *Études fl. Congo* 1: 217 (1896); Burkill in *Fl. trop. afr.* 5: 40 (1899); Durand & Durand, *Syll. fl. congol.*: 417 (1909); Benoist in *Bull. Soc. Bot. France* 60: 335 (1913); Chevalier, *Explor. bot. Afrique occ. franç.* 1: 493 (1920); Hutchinson & Dalziel in *Fl. W. trop. Afr.* 2: 254 (1931); Heine in *Fl. W. trop. Afr.* 2nd ed., 2: 406 (1963). Type: Nigeria, Benin, Agathon, *Palisot de Beauvois* s.n. (G!-lectotype; G!-isolectotypes).

Belantheria belvisiana Nees in *DC. Prodr.* 11: 96 (1847). Type: as for *B. owariensis*.

Brillantaisia patula T. Anderson in *J. Proc. Linn. Soc. Bot.* 7: 21 (1864); Burkill in *Fl. trop. afr.* 5: 41 (1899); Hiern in *Cat. afr. pl.* 1: 807 (1900); De Wild., *Études fl. Bas-Moyen-Congo* 1: 314 (1903–1906); Durand & Durand, *Syll. fl. congol.*: 417 (1909); Benoist in *Bull. Soc. Bot. France* 60: 335 (1913); De Wild., *Contr. Fl. Katanga* 1: 143 & 2: 144 (1913); Mildbraed, *Wiss. Erg. zweit. deut. Zentr.-Afr. Exped., Bot.* (1922); Hutchinson & Dalziel in *Fl. W. trop. Afr.* 2: 254 (1931); Exell, *Cat. pl. S. Tomé*: 260 (1944); Robyns, *Fl. parc. nat. Albert.* 2: 269–270 (1947); Heine in *Fl. W. trop. Afr.* 2nd ed., 2: 406 (1963); Heine in *Fl. Gabon* 13: 94, pl. 19, figs 1–6 (1966); Champluvier in *Fl. Rwanda* 3: 444–448 (1985). Type: Congo, *Smith* s.n. (K!-holotype; BM!, P!-isotypes).

B. alata T. Anderson ex Oliv. in *Trans. Linn. Soc. London* 29: 125 (1875); S. Moore in *J. Bot.* 18: 197 (1880); Durand & Schinz, *Études fl. Congo* 1: 216–217 (1896); Durand & De Wild., in *Bull. Soc. Roy. Bot. Belgique* 36: 83 (1897); De Wild., *Miss. Ém. Laurent* 1: 182 (1905); De Wild., *Études fl. Bas-Moyen-Congo* 1: 314 (1903–1906); De Wild., *Contr. Fl. Katanga* 1: 143 (1913). Type: Uganda, Unyoro, *Speke & Grant* 583 (K!-holotype).

B. salviiflora Lindau in *Bot. Jahrb. Syst.* 17: 101 (1893); Burkill in *Fl. trop. afr.* 5: 41 (1899); Benoist in *Bull. Soc. Bot. France* 60:



Map 2 The distribution of *Brillantaisia stenopteris* Sidwell.



Fig. 11 *Brillantaisia stenopteris* Sidwell. Habit $\times 0.7$; B. Corolla dissection showing androecium $\times 2.5$; C. Gynoecium and calyx $\times 2.5$; D. Bract and bractlets $\times 3$.

336 (1913). Type: Togo, Bismarckburg, Büttner 341 (B⁺-holotype).

B. nitens Lindau in *Bot. Jahrb. Syst.* **17**: 102 (1893); Burkill in *Fl. trop. afr.* **5**: 41 (1899); Lindau in *Wiss. Erg. deut. Zentr.-Afr. Exped., Bot.* **2**: 292 (1911); Benoist in *Bull. Soc. Bot. Fr.* **60**: 336 (1913); Mildbraed, *Wiss. Erg. zweit. deut. Zentr.-Afr. Exped., Bot.* (1922); Hutchinson & Dalziel in *Fl. W. trop. Afr.* **2**: 254 (1931); Robyns, *Fl. parc. nat. Albert.* **2**: 270–272 (1947); Heine in *Fl. W. trop. Afr.* 2nd ed., **2**: 406 (1963); Blundell, *Wild fl. Kenya*: 104 (1982); Champluvier in *Fl. Rwanda* **3**: 448 (1985); Blundell, *Wild fl. E. Afr.*: 389 (1987). Type: Cameroon, W. of Buea, Preuss 847 (B⁺-holotype; K[!]-isotype).

B. dewevrei De Wild. & Th. Dur. in Durand & De Wild., in *Bull. Soc. Roy. Bot. Belgique* **38**: 44–45 (1899); Burkill in *Fl. trop. afr.* **5**: 51 (1899); De Wild. & Durand, *Ann. Mus. Congo Sér. 3 Bot.* **1**: 174–175 (1901); De Wild. & Durand in *Bull. Herb. Boissier* **1**: 833 (1901); Durand & Durand, *Syll. fl. congol.*: 416–417 (1909). Type: Congo, between Lukolela and Gombi, Dewevre s.n. (BR[!]-holotype).

B. nyanzarum Burkill in *Fl. trop. afr.* **5**: 39 (1899); Robyns, *Fl. parc. nat. Albert.* **2**: 272 (1947); Andrews, *Fl. pl. Sudan* **3**: 171 (1956); Agnew, *Upl. Kenya wild fls.*: 583 & 584 (1974); Synnott in *Comm. Forestry Inst. Occ. Papers* **27**: 68 (1985). Type: Kenya, Kavirondo, Scott-Elliott 6999 (K[!]-holotype).

B. leonensis Burkill in *Fl. trop. afr.* **5**: 41 (1899); Benoist in *Bull. Soc. Bot. France* **60**: 335 (1913); Hutchinson & Dalziel in *Fl. W. Trop. Afr.* **2**: 254 (1931). Syntypes: Sierra Leone, Scott-Elliott 3990a (K[!]), Windwood Reade s.n. (K[!]), Don s.n. (BM[!]).

B. patula var. *welwitschii* Burkill in *Fl. trop. afr.* **5**: 41 (1899); Hiern in *Cat. afr. pl.* **1**: 807 (1900). Syntypes: Angola, near Sange, Quiapoza and Cuango Rivers, Welwitsch 5149 (BM[!]), Quibolo, Welwitsch 5182 (BM[!], K[!], P[!]).

B. mahonii C.B. Clarke in *Bull. Misc. Inform.* 1906: 251 (1906); S. Moore in *J. Bot.* **45**: 89 (1907); Lind, *Comm. fl. pl. Uganda*: 140, fig. 82 (1962). Type: Uganda, Entebbe, Mahon s.n. (K[!]-holotype).

B. bauchiensis Hutchinson & Dalziel in *Fl. W. trop. Afr.* **2**: 253 (1931); Hutchinson & Dalziel *Fl. W. trop. Afr.* 2nd ed., **2**: 407. Syntypes: Nigeria, Bauchi Plateau, Lely P129 (K[!]), Dent Young 195 (K[!]).

Icones: *P. Beauv., Flore d'Oware* **2**: t. 100 fig. 2 (1818); Anderson in *Trans. Linn. Soc. London* **29**: pl. 124 (1875); Hooker in *Bot. Mag.*: 79: t. 4717 (1853) excluding glabrous fruit; Heine in *Fl. Gabon, Acanthacées*: **13**: pl. 19 figs 1–6 (1966); Agnew, *Upl. Kenya wild fls.*: 584 (1974); Blundell, *Wild fl. Kenya*: pl. 264 (1982); Champluvier in *Fl. Rwanda* **3**: fig. 139: 2, 3A–3D (1985); Blundell, *Wild fl. E. Afr.*: pl. 849 (1987).

Herbs or woody herbs to 1–3(–4) m tall, viscid, often aromatic. Stems 1–8(–15) mm in diameter, glabrous or pubescent towards apex. Leaves ovate to broadly ovate (35–)50–140(–210) × (25–)40–120(–185) mm; leaf base cordate to cuneate; apex acuminate sometimes markedly so; margin toothed, usually irregularly serrate, crenate towards apex with or without secondary toothings; eglandular pubescent above and below, sometimes densely pubescent; lateral veins 6–19 each side of the midrib; petiole (10–)30–90(–130) mm long, lamina decurrent in upper ½–¾ length of petiole, occasionally entire length of petiole. Inflorescence a many flowered terminal panicle (9–)15–40(–60) cm long with 4–18 nodes; rachis glandular pubescent. Bracts ovate, (3–)20–50(–75) × (5–)15–25(–40) mm, usually falling early; bractlets linear oblong, to 20 × 5 mm, eglandular pubescent. Sepals subequal to unequal, linear, (5–)9–15(–22) × 1 mm long, rounded to slightly spatulate at the apex, glandular pubescent. Corolla

pale purple to deep blue-purple often with yellow markings in throat; tube (5–)7–10(–14) × 2–6 mm long; upper lip (13–)18–30(–60) mm long, outer surface of upper lip glandular pubescent; lower lip (14–)18–30(55) mm long, glabrous; apical lobes (1–)2–5(–10) mm long. Androecium with filaments (20–)25–35(–40) mm long; anthers (2–)5–7(–10) mm long; staminodes (10–)15–25(–30) mm long with small vestigial anther at the apex. Gynoecium with style (15–)20–35(–45) mm long; stigma 2–4(–6) mm long; ovary 3–7 mm long, pubescent. Capsule (15–)18–26(–33) × 2–3 mm with (10–)12–18(–24) seeds per locule; covered with eglandular and glandular trichomes.

DISTRIBUTION. Throughout tropical Africa.

HABITAT. Moist montane forest particularly in open shady places where competition is reduced in recently disturbed areas; 600–1600 m.

SELECTED COLLECTIONS

SIERRA LEONE: 18 November 1965, Adam 22109 (MO, P); 2 January 1966, Adam 22916 (MO, P); 27 November 1965, Adam 27084 (MO); Mt. Nimba, 14 December 1966, Bos 2397 (WAG); 8°25'W 7°32'N, 18 December 1967, Geerling & Bockdam 1859 (C, MO, WAG); LIBERIA: 10 January 1965, Adam 20549 (BR, K, MO, P, UPS); Grand Cape Mount Co., 21 December 1947, Baldwin 10778 (K, MO); 6 November 1947, Baldwin 10182 (K, MO); Loffa country, 21 December 1966, Bos 2552 (K, WAG). IVORY COAST: 24 November 1909, Chevalier 22421 (P); 20 km de Man sur route de Danané, 23 November 1956, de Wilde 859 (WAG); Mont Tonkoui, près de Man, 3 December 1985, Ake Assi 17170 (G). GHANA: Bauchi Plateau, 17 April 1955, Morton K416 (K, WAG); Kofordua, Dalziel 148 (C, E, K, M, MO, PRE, WAG). NIGERIA: Mandaga, Nambila Plateau, 4 January 1955, Latilo & Daramola FHI 28992 (FHO); Shasha Forest Reserve, Richards 3108 (BM, MO, NY); 11 December 1976, Ariwaodo 33. CAMEROON: 13 February 1927, Dalziel 8232 (US); Buea, Preuss 1029 (BM, M); Dschang, December 1938, Jacques-Felix 2600 (P); 31 km on Ebolowa-Ambam Road, 1 September 1974, de Wilde 7544 (WAG); Lake Oku, 6°13'N 10°28'E, Thomas 4381 (MO, YA); GABON: Woleu-Ntem Province, 14 November 1933, Le Testu 9395 (BR); CENTRAL AFRICAN REPUBLIC: 10 December 1936, Eckendorf 73 (P); CONGO: Sangha, 2°N 13°55'E, 27 November 1991, Thomas 9005 (MO); DEMOCRATIC REPUBLIC OF THE CONGO: 12 January 1914, Bequaert 1905 (BR); Kivu, Lac Mokoto, 27 July 1953, van der Ben 648 (BR); Yangambi region, Yabahondo village, October 1952, Germain 8141 (BR, W, Z). RWANDA: Rwaza, SE de Ruhengeri, 23 February 1972, Auquier 2684 (BR). BURUNDI: 2 June 1969, Lewalle 3795 (BR). UGANDA: Bigera River, 3 August 1906, Bagshawe 1131 (BM). KENYA: December 1933, Dale 3208 (BR, FHO); January 1932, Brodhurst-Hill 693 (Z). TANZANIA: 26 January 1991, Kayombo 1072 (MO). ANGOLA: 24 June 1958, Montiero, Santos & Murta 205 (PRE).

Brillantaisia owariensis is the most widespread and variable of all species in the genus and has caused many problems of species delimitation for botanists over the years. After extensive herbarium studies, supplemented by field work in Cameroon and Tanzania, I consider it impossible to split this group into discrete taxa and recognize it as a very diverse 'ochlo-species' (sensu White, 1962: 79) and accept that, although unsatisfactory, this is the only viable option without further extensive studies in the field. *Brillantaisia owariensis* sensu meo encompasses all fairly robust, woody *Brillantaisia* plants with a paniculate inflorescence, toothed leaves with a winged petiole and pubescent fruit. Morphological variation within the group appears more pronounced in certain parts of Africa. In East Africa, for example, clear morphological differences can be observed between different isolated groups and two representative specimens may look nothing like one another when the extremes of morphological variation are observed. However, when morphological variation is studied across the whole of Africa, character differences break down and distinct groups cannot be distinguished.

Variable characters include leaf shape, leaf base shape, leaf margin, number of lateral veins, calyx shape, inflorescence density, flower size, fruit length/width and fruit pubescence. The morphological variation within *Brillantaisia owariensis* is informally described below in terms of two main groups: the *nitens* group and the *patula* group.

Plants which tend to differ from typical *B. owariensis* in possessing rather finely toothed leaves, a somewhat narrow petiole wing, larger number of lateral nerves and a relatively dense inflorescence could be assigned to the *nitens* part of *Brillantaisia owariensis*. *Brillantaisia nitens* was described by Lindau (1893) as being distinct from all other Brillantasias due to the leaf pubescence, which is comparatively dense for the genus. Plants with characters of the *nitens* group tend to occur in the forests of Cameroon and further west in tropical Africa. Plants that are slightly more robust than typical *Brillantaisia owariensis*, with velvety-tomentose leaves, have previously been distinguished as *Brillantaisia bauchiensis* in Nigeria and *B. leonensis* in Sierra Leone. Specimens with longer calyx lobes and sub-persistent bracts were previously assigned to *B. mahonii*. Specimens from East Africa that generally have the same morphological characters as those of the *nitens* group, but differ in the presence of more persistent bracts, have often been identified as *B. nyanzarum*.

The *patula* group: The most distinct node of variation within *Brillantaisia owariensis* is seen on specimens that can be informally described as the *patula* group. These plants have a very open, lax, 'zigzag' inflorescence architecture and often have large flowers and a linear calyx. Specimens with these characteristics do not seem to be restricted to one area of Africa and have been collected from Guinea to Zaire and on São Tomé. Most *patula* specimens have been collected from the Congo basin. Leaves of the *patula* 'node' often, but not always, have a distinct wing to the base of the petiole (Mocquery's 115, Z; Richards 3018, BM) which is occasionally amplexicaul.

6. *Brillantaisia kirungae* Lindau in *Götzen, Durch Afrika von Ost nach West, Sonderabdr.*: 9 (1896); Burkill in *Fl. trop. afr.* 5: 42 (1899); Durand & Durand, *Syll. fl. congol.*: 417 (1909); Robyns, *Fl. parc nat. Albert* 2: 269 (1947). Type: Zaire, Mount Kirunga, von Götzen 48 (B⁺-holotype).

Fig. 12.

B. ulugurica Lindau in *Bot. Jahrb. Syst.* 22: 112 (1897); Burkill in *Fl. trop. afr.* 5: 43 (1899); Brenan & Greenway, *Checklist brit. empire 5 Tangan. terr.* 2: 6 (1949). Syntypes: Tanzania, Uluguru Mts, Stuhlmann 8850 (B⁺) & Stuhlmann 9224 (B⁺)

B. subulugurica Burkill in *Fl. trop. afr.* 5: 42 (1899); Binns, *Checklist herb. fl. Malawi*: 12 (1968). Type: Mozambique, Makua, Namuli Hills, Last s.n. (K[!]-holotype).

B. grandidentata S. Moore in *J. Bot.* 45: 331 (1907). Type: Uganda, Toro, Fort Portal, Bagshawe 1270 (BM[!]-holotype).

B. cicatricosa var. *kivuensis* Mildbr. in *Bull. Jard. Bot. État* 17: 86 (1943); Robyns, *Fl. parc nat. Albert* 2: 270 (1947). Type: Zaire, Lake Magera, de Witte 1434 (BR[!]-holotype; BR[!]-isotype).

B. nitens sensu Agnew, *Upl. Kenya wild fls*: 583 (1974), non Lindau (1893).

Icones: Champluvier in *Fl. Rwanda* 3: fig. 139, 1A–1D (1985); Fischer & Hinkel, *Nat. env. Rwanda*: fig. 68 (1992).

Stout shrubby herbs 1–2 m tall to shrubs or small trees 2–5(–7) m tall with bole 1.4 m high and 12 cm diameter, viscid and sometimes aromatic. *Stems* erect, 5–20(–120) mm across, shortly puberulent. *Leaves*, broadly ovate 60–320 × 50–240 mm; leaf base cordate or

truncate to attenuate or cuneate; apex acute to acuminate; margin irregularly toothed, teeth single or double, smaller becoming crenate towards the apex, rarely entire; puberulous; lateral veins 7–13 each side of the margin, lower laterals closer together; petiole (0–)10–140 mm long, lamina gradually decurrent on top ½–¾ of petiole, upper pair of leaves at base of inflorescence sessile. *Inflorescence* a terminal thyrse 15–25(–40) cm long, lateral branches erect, at 30–50 degrees to the main rachis, flowers crowded at end of lateral branches; rachis shortly pubescent; trichomes, red-brown, non glandular, sometimes straggly purple trichomes. *Bracts* broadly ovate to ovate, occasionally elliptic, base slightly amplexicaul, apex rounded to acute; bractlets ovate(-linear), falling late or remaining in fruit. *Sepals* unequal, larger upper sepal linear, rounded at tip or slightly spatulate, (8–)10–14(–19) × 1–3(–5) mm, often twice as wide as lateral sepals (clearly seen in bud), occasionally very large; smaller lateral sepals linear 8–15 × 1 mm; densely pubescent dorsally. *Corolla* pale blue to bright blue-purple or pink-purple, with darker markings on lower lip; corolla tube 6–10 × 3–6 mm, occasionally inflated; upper lip 19–35 × 6–10 mm, evenly covered in dense, eglandular and glandular trichomes; lower lip 19–40 × 10–18(–25) mm, ridged on upper surface; apical lobes triangular, 3–10 × 2–8 mm. *Androecium* with filaments 20–25(–30) mm long; anthers (3–)5–8 mm long; staminodes 8–12 mm, very slender often with well developed vestigial anther. *Gynoecium* with style 25–40 mm long; stigma 2 mm long; ovary 5–10 mm, covered in tangled glandular trichomes, sometimes also with non glandular trichomes. *Capsule* 30–40 × 2–5 mm with 8–10(–16) seeds per locule; black, glandular puberulous. Specimens often drying black.

DISTRIBUTION. East and central Africa, from Kenya south to Zimbabwe and Mozambique, west to Uganda and Eastern Zaire.

HABITAT. In gaps in mid altitude and montane forest, forming thickets, often along streams. Very local; 1000–3500 m.

SELECTED COLLECTIONS

DEMOCRATIC REPUBLIC OF THE CONGO: Kivu, 27 July 1959, *Cambridge Congo Expedition* 146 (BM, LISC, US). RWANDA: Parc des Volcans, 27 July 1974, *Van der Veken* 10350 (BR). BURUNDI: Rwegura, 29 May 1969, *Lewalle* 3640 (BR, G); Bubanza, 22 June 1980, *Reekmans* 9408 (K, MO, UPS). SUDAN: Imatong Mts, Gilo Village, 8 November 1980, *Friis & Vollesen* 58 (C). UGANDA: Ruwenzori Mts, Namwamba Valley, 17 January 1935, *Taylor* 3156 (BM, MO, NY, S). KENYA: 18 March 1977, *Faden & Faden* 77/919 (BR, US, WAG). TANZANIA: Rungwe, Kiwara River, 9 August 1949, *Greenway & Eggeling* 8394 (PRE); Morogoro, Bunduki, 17 August 1951, *Greenway & Eggeling* 8594 (FHO); Nugwi River, 19 August 1952, *Carmichael* 102 (FHO); Mbisi Mts, 17 June 1960, *Leach & Brunton* 10069 (SRGH); Ufipa, 6 August 1960, *Richards* 12983 (SRGH); Kilosa District, Ukaguru Mts, 7 August 1972, *Mabberley* 1403 (K), Mufindi Tea Estate, 17 August 1984, *Bridson & Lovett* 544 (MO). MOZAMBIQUE: Namuli Peaks, 26 July 1962, *Leach & Schelpe* 11470 (LISC, SRGH); MALAWI: Nchisi Mts, 4 September 1929, *Burtt Davy* 1228 (FHO); Kafwimba Forest, 4 July 1973, *Pawek* 6978 (C, PRE, SRGH, UPS). ZIMBABWE: Ngoruma reserve, 14 August 1962, *Plowes* 2261 (LISC, SRGH); Vumba, 20 September 1968, *Müller* 802 (SRGH).

Brillantaisia kirungae is the largest and most woody of the species of *Brillantaisia* and is easily recognized by the woody or shrubby habit; highly irregularly toothed leaves; large flowers in a crowded erect inflorescence; broad upper calyx lobe and large, few-seeded fruit. This species is rather variable in leaf shape and tooting (most collections lack the larger lower leaves, so measurements given above need refining after more field studies); the degree of contraction of the inflorescence; density of the indumentum on both the inflorescence and fruit; and flower size, particularly the size of the lobes at the apex of the lower lip. Previous treatments of *Brillantaisia kirungae* have all divided it into more than one species. For example,



Fig. 12 *Brillantaisia kirungae* Lindau. A. Habit $\times 0.7$; B. Lower leaf $\times 0.7$. C. Corolla dissection showing androecium $\times 1.4$; D. Gynoecium $\times 1.4$. E. Capsule $\times 1.4$; F. Bract and bractlets $\times 1$.

Burkill (1899) recognized four species: *Brillantaisia cicatricosa* with subglabrous sepals and numerous seeds; *B. kirungae* with lanceolate bracts; *B. ulugurica* with large flowers and large lobes at the apex of the lower corolla lip and a new species, *B. subulugurica* which was considered distinct from *B. ulugurica* due to the shorter corolla tube. More recently, Champluvier (1985) recognized two species, *B. kirungae* and *B. cicatricosa*, separated on the size of the upper sepal. All of the characters used by previous authors to divide this species are continuously variable when the entire geographical variation of the group is accounted for. In his treatment of the genus for the *Flora of Tropical East Africa* and *Flora Zambesiaca*, Vollesen (in prep a & b) recognizes two species within this group, *B. cicatricosa* and *B. ulugurica*. He considers plants of *B. cicatricosa* to have irregularly large-toothed leaves; smaller lower corolla lip lobes; smaller seeds, to lack glandular trichomes on the fruit and to have a more northerly distribution from Kenya, Uganda, Burundi, Rwanda and Zaire. *Brillantaisia ulugurica sensu* Vollesen is recognized as distinct on the basis of smaller irregular teeth on the leaves; leaf margin becoming entire towards the apex; larger lobes on the lower corolla lip; larger seeds; both glandular and non glandular trichomes on the fruit; and a more widespread geographical range in Uganda, Burundi, Zaire, Tanzania, Malawi, Mozambique, Zimbabwe and Zambia. Two characters used by Vollesen to distinguish *B. cicatricosa* from *B. ulugurica* are not overlapping or continuous in his species descriptions: seed size and fruit hair type. I have studied the two species across their entire range which includes specimens from Sudan and Angola. It appears that although some 'cicatricosa-like' specimens do have smaller flowers, deeply toothed leaves with a more cordate base, smaller seeds and no glandular trichomes on the capsule, these characters are continuously variable and there is no morphological data to support separation of the two species.

A new species from Tanzania was mentioned by Vollesen (in prep. a) as closely related to *Brillantaisia ulugurica*. Plants belonging to the new putative new species were recognized primarily by the presence of long, rather synthetic looking, purple, eglandular trichomes on the panicle and calyx, and by the larger capsule (no measurements given). Several intermediates between *B. ulugurica sensu* Vollesen, with short puberulent trichomes on the panicle and short glandular and eglandular trichomes on the calyx, and the purple haired *sp. nov.* cf. *B. ulugurica* have been studied (e.g. MOZAMBIQUE: *Leach & Schelpe* 11470; MALAWI: *Chapman & Chapman* 9271 Mt Mulanje; *Burt Davy* 1228) and I consider the variation to represent one species. Within the single species recognized in this treatment, plants with a more lax inflorescence, more slender sepals and smaller flowers tend to occur further north-north west (SUDAN, Gilo Village, *Friis & Vollesen* 58 C; RWANDA, Parc des Volcans, *Van der Veken* 10350, BR; UGANDA, Kanaba Pass, *Makerere College* 29) whereas larger more robust plants are more commonly from Malawi and Mozambique.

Typification of this species is somewhat problematic as mentioned by Champluvier (1985). I disagree with her decision to retain the epithet *cicatricosa*. Specimens of *B. kirungae sensu meo* have historically been named as *B. cicatricosa*, *B. kirungae*, or *B. ulugurica*, however, the type specimens of all three of these names were destroyed in Berlin. The protologue of the earliest name, *B. cicatricosa* Lindau, is somewhat ambiguous and does not fit the species description above. Although the Latin diagnosis of *B. cicatricosa* mentions the large upper sepal of this species, several characters do not fit the group well, notably subglabrous sepals and 16–20 seeds in the capsule. The original description of *B. cicatricosa* Lindau mentioned that the species was close to *B. pubescens* T. Anders., however without a type specimen of *B. cicatricosa* the variation observed by Lindau when he made this seemingly misplaced statement cannot be

checked. It may well be the case that Lindau based his observation on the illustration of Fitch in Anderson (1875) which has caused considerable confusion in *Brillantaisia* (see p. 86). *Brillantaisia cicatricosa sensu* Burkill (1899) adds to the ambiguity of this name as he describes the species as having entire, glabrous leaves, a loose inflorescence, nearly glabrous sepals and 16–20 seeds, whereas the species recognized here has irregularly toothed pubescent leaves and a crowded inflorescence. A variety of *B. cicatricosa* Lindau was formally recognized by Mildbraed (1943) on the presence of glandular trichomes on the calyx. This taxon is illustrated in *Flore du Rwanda* (Champluvier, 1985) and clearly falls within *B. kirungae* as delimited here. However, I am not certain that Mildbraed saw the type specimens of *B. cicatricosa* or that he understood Lindau's concept of that species. Therefore, as the protologue of *B. cicatricosa* Lindau is ambiguous and the description of *B. cicatricosa* by Burkill does not fit this species, I treat this name as dubious, and use the second earliest name, *B. kirungae*, for this species.

7. ***Brillantaisia vogeliana*** (Nees) Benth. in *Hooker, Niger Fl.*: 477 (1849); Anderson in *Journ. Linn. Soc. Bot.* 7: 21 (1864); Burkill in *Fl. trop. afr.* 5: 40 (1899); Benoist in *Bull. Soc. Bot. France* 60: 335 (1913); Hutchinson & Dalziel in *Fl. W. trop. Afr.* 2: 254 (1931); Exell, *Cat. pl. S. Tome*: 260 (1944); Mildbraed, *Wiss. Erg. zweit. deut. Zentr.-Afr. Exped., Bot.*: 192 (1922); Robyns, *Fl. parc. nat. Albert* 2: 272 (1947); Heine in *Fl. W. trop. Afr.* 2nd ed., 2: 406 (1963); Heine in *Fl. Gabon* 13: 92 (1966). Type: Fernando Po, *Vogel* 179 (K!-holotype; K!-isotype).

Fig. 13.

- Leucoraphis vogeliana* Nees, in DC., *Prodr.* 11: 97 (1847).
Brillantaisia molleri Lindau in *Bot. Jahrb. Syst.* 17: 99 (1893). Type: São Tomé, *Möller* 33 (87) (B⁺-holotype; COI!, K!-isotypes).
B. preussii Lindau in *Bot. Jahrb. Syst.* 17: 100 (1893). Syntypes: Cameroon, Barombi, *Preuss* 320 (K!-isotype) Buea, *Preuss* 998 (BM!, K!-isotypes)
B. soyauxii Lindau in *Bot. Jahrb. Syst.* 17: 101 (1893); Burkill in *Fl. trop. Afr.* 5: 39 (1899); Benoist in *Bull. Soc. Bot. France* 60: 335 (1913); non Heine in *Fl. Gabon* 13: 84 (1966). Type: Gabon, Munda, Sibange Farm, *Soyaux* 454 (B⁺-holotype; E!, H!, US!, WAG!-isotypes).
B. schumanniana Lindau in *Bot. Jahrb. Syst.* 17: 102–103 (1893). Type: Cameroon, *Braun* 47 (B⁺-holotype).

Icones: Heine in *Fl. Gabon* 13: pl. 18, figs 1–6 (1966); Heine, in *Fl. W. trop. Afr.* 2nd ed., 2: 406, fig. 300 (1963).

Erect herbs to 0.2–1 m tall. *Stems* erect, 2–4 mm in diameter, branching near base, leaf petioles fused across each node, glabrous or shortly pubescent with a fringe of trichomes at the nodes. *Leaves* ovate to broadly ovate 35–100(–110) × 45–120(–150) mm, papery, bright green, paler below, evenly pilose; leaf base truncate or cordate, occasionally shortly attenuate; apex slightly acuminate, rounded; margin irregularly serrated, dentate at base of lamina around the widest part of the leaf, crenate towards the apex of the leaf; lateral veins 7–13 each side of midrib, prominent; petiole (30–)40–120 mm, lamina decurrent on upper third of petiole, wing often toothed at top. *Inflorescence* a terminal lax thyse (8–)12–20(–30) cm long, with smaller lateral inflorescences in axils of lower leaves; rachis shortly glandular pubescent with slender non glandular trichomes. *Bracts* to 7 × 15 mm, often falling early; bractlets linear elliptic to 2 mm long, glabrous with fringe of irregular glandular trichomes. *Sepals* unequal, slightly spatulate, larger upper sepal 6–15 mm long, smaller lateral sepals 6–10(–12) mm long, viscid glandular pubescent. *Corolla* clear



Fig. 13 *Brillantaisia vogeliana* (Nees) Benth. A. Habit $\times 0.7$; B. Corolla dissection showing androecium $\times 3$; C. Capsule $\times 2$; D. Gynoecium $\times 3$; E. Bract and bractlets $\times 1$.

mauve-violet, white in throat with lateral yellow spots; corolla tube paler, tube 2–4 × 5–10 mm, slightly shorter than the calyx lobes; upper lip 11–15(–25) mm covered with glandular and non glandular trichomes on outer surface, more so towards the apex; lower lip 10–15(–25) mm long; apical lobes to 1 × 1 mm, central tooth broader than the laterals, glabrous. *Androecium* with filaments 12–17(–24) mm long, glabrous; anthers 2–4(–6) mm long; staminodes 6–10 mm long, flattened at tip to vestigial anther, glabrous. *Gynoeceum* with style 15–20 mm long; stigma 1.5–3 mm long; ovary 3–4 mm long. *Capsule* (10–)17–21(–24) × 1–2 mm with 20–24 seeds in each locule, indumentum of slender white non glandular trichomes and short glandular trichomes.

DISTRIBUTION. Throughout West Africa and on the islands of the Gulf of Guinea across Central African Republic and Congo to Sudan, Uganda and Kenya.

HABITAT. A weedy species common in wasteland, clearings, plantations and along roadsides; 60–1200 m.

SELECTED COLLECTIONS

IVORY COAST: Mont Momi, 29 October 1966, *Ake Assi* 9136 (G). GHANA: Atewa Range N. of Kibi, 3 November 1990, *Manktelow, Steiner & Amponsah* 89 (UPS). CAMEROON: N'Kolbisson, 3 November 1963, *de Wilde & de Wilde-Duyffes* 1130 (K, MO, WAG, YA); Nkolbison, 8 km W. of Yaounde, Mount Minloua, 19 November 1964, *Raynal* 11964 (P); 17 km along Kribi-Lolodorf road, 22 September 1969, *Bos* 5387 (C, K, MO, PRE, UPS, WAG, YA); Chutes de Ntem, 40 km ESE of Campo, 10 December 1979, *Letouzey* 15340 (P); Sao Nicolau, 9 January 1980, *de Wilde, Arends & Groenendijk* 3 (WAG); crossing of road from S. Joao dos Angolares to Ribeira Peize, 12 January 1980, *de Wilde, Arends & Groenendijk* 95 (WAG); Kumba area, 13 October 1984, *Thomas & Nemba* 4048 (MO). BIOCCO: October 1911, *Mildbraed* 7028 (H). CENTRAL AFRICAN REPUBLIC: 27 km S. of Nola, 29 November 1965, *Leeuwenberg* 7100 (BM, C, K, LISC, WAG). CONGO: Solongo, 22 March 1959, *Everard* 6002 (PRE); Piste Meya – Mpassa, 28 April 1965, *Farron* 4085 (P). SÃO TOMÉ: Famosa, 5 January 1949, *Espirito Santo* 68 (BM); Monte Cape, 5 March 1968, *Espirito Santo* 4298 (LISC); road from Nora Moka to Manuel Jorge River, 15 October 1993, *Figueiredo & Arriegas* 33 (FHO, K, LISC). GABON: Belinga Mines de Fer, 25 June 1966, *Halle* 4058 (P); Boka-Boka, Mount Bengoué, 4 March 1979, *Florence* 1706 (P); Woleu-Ntem, 2 May 1986, *Louis* 2077 (WAG); 10 km from Belinga, 5 December 1986, *Bos, van der Laan & Nzabi* 10755 (K, US, WAG). DEMOCRATIC REPUBLIC OF THE CONGO: Dyuana, Parc National Albert, 11 October 1955, *de Witte* 12827 (MO). SUDAN: Imatong Mountains, Talanga, 1 December 1980, *Friis & Vollesen* 612 (C). UGANDA: Budongo forest, December 1935, *Eggeling* 3323 (K); Mabira forest, 8 November 1938, *Loveridge* 25 (K). KENYA: Kakamega forest, 11 December 1956, *Verdcourt* 1683 (K).

Brillantaisia vogeliana is often locally abundant as a weed along road and path sides and in clearings in secondary vegetation, small farms, plantations, etc. It is readily identified by leaves that are often cordiform, characteristically irregularly toothed and often with a toothed petiole; the highly branched inflorescence; relatively small flowers which are usually a clear mauve-violet and paler in the throat, and the pubescent fruit which have numerous seeds per locule. This species might be confused with *B. owariensis*, on the basis of the lax inflorescence and toothed leaves, and Vollesen tends to place East African specimens with rounded teeth and a wider inflorescence into that species. Plants of *B. vogeliana* differ, from those of *B. owariensis*, in possessing thinner, papery leaves with a more dentate, irregular leaf margin and pronounced dentate margin at the apex of the petiole wing; a more highly branched, slender inflorescence; smaller flowers and fruit with more seeds. A few specimens of *B. vogeliana* from the Congo basin have small flowers but larger leaves than typical *B. vogeliana* and seem to approach *B. owariensis*. White-flowered

forms of this species are fairly common. Exell (1944: 261) noted the two colour forms and stated 'They seem to be identical except for the flower-colour and they always grow together, the purple-flowered form being rather more common'.

8. *Brillantaisia lamium* (Nees) Benth. in *Hooker, Niger Fl.*: 477 (1849); Burkill in *Fl. trop. Afr.* 5: 38 (1899); Hiern in *Cat. afr. pl.* 1: 807 (1900); Durand & Durand, *Syll. fl. congol.*: 417 (1909); Benoist in *Bull. Soc. Bot. France* 60: 334 (1913); Chevalier, *Explor. bot. Afrique occ. franç.* 1: 493 (1920); Mildbraed, *Wiss. Erg. zweit. Zentr.-Afr. Exped., Bot.* 2: 90 (1922); Hutchinson & Dalziel in *Fl. W. trop. Afr.* 2: 254 (1931); Exell in *Cat. pl. S. Tome*: 260 (1944); Heine, in *Fl. W. trop. Afr.* 2nd ed., 2: 406 (1963); Heine in *Fl. Gabon* 13: 88 (1966). Type: *Ansell* 1842 (K!-lectotype) (P!-isolectotype).

Fig. 14.

Leucoraphis lamium Nees in DC., *Prodr.* 11: 97 (1847). Type: As for *Brillantaisia lamium*.

Brillantaisia palisotii Lindau in *Bot. Jahrb. Syst.* 17: 99 (1893); Henriques in *Bol. Soc. Brot.* 10: 146 (1893). Lindau in *Nat. Pflanzenfam.* 4(3b): 296, fig. 119 (1895). Syntypes: Sierra Leone, Freetown, *Preuss* 16 (B); Sierra Leone, Freetown, *Afzelius* s.n. (UPS!); Togo, Bismarckburg, *Büttner* 231 (B), *Büttner* 320 (B); Cameroon, Mungo, *Buchholz* s.n. (BM!); São Tomé, *Quintas* 1235(88) (BM!, BR!, COI, Z!), *Quintas* 1132(89) (COI); Angola, Luanda, *Pogge* 1123 (?).

B. eminii Lindau in *Bot. Jahrb. Syst.* 17: 103 (1893); Lindau in *Pflanzenw. Ost-Afr. C.* 366 (1895d); Burkill in *Fl. trop. Afr.* 5: 38 (1899); Jex-Blake, *Wild fl. Kenya*: 103, fig. 84 (1948); Brenan & Greenway, *Checklist brit. empire 5 Tangan. Terr.* 2: 5 (1949); Andrews, *Fl. pl. Sudan* 3: 172 (1956); Synnott, *Comm. forest. inst. occ. papers* 27: 68 (1985). Syntypes: Tanzania, Bukoba, *Stuhlmann* 3664 (K!); *Stuhlmann* 3995 (B⁺).

B. owariensis sensu Hook. in *Bot. Mag.*: t. 4717, fig. 3 (1853); T. Anderson in *Journ. Linn. Soc. Bot.* 7: 339 (1863); Engler in *Bot. Jahrb. Syst.* 7: 339 (1886), non P. Beauv. (1818).

B. subcordata De Wild. & T. Durand in: T. Durand & De Wild. *Bull. Soc. Roy. Bot. Belgique* 38: 44–45 (1899); De Wild. & Durand *Ann. Mus. Congo* 1: 175–176 (1901); De Wild. *Miss. Ém. Laurent* 1: 182, t. 45 (1905); Durand & Durand, *Syll. fl. congol.*: 418 (1909). Type: Zaire, Bokakata, *Dewevre* 802 (BR!-syntypes).

B. subcordata var. *macrophylla* De Wild. & T. Durand. in *Contrib. fl. Congo* 1, 2: 47 (1900). Type: Locality uncertain, village on the Congo river, *Duchesne* 13 (BR!-holotype).

Icones: Lindau in *Nat. Pflanzenfam.* 4(3b): fig. 119A–G (1895); Heine, in *Fl. W. trop. Afr.* 2nd ed., 2: fig. 300 (1963); Heine, *Fl. Gabon*: 13: pl. 17 figs 4–8 (1966).

Perennial herbs (7–)20–100(–200) cm tall, creeping to erect, occasionally climbing with adventitious roots at nodes. *Stems* 4.5 mm in diameter, occasionally with longitudinal wings on angles, glabrous to velvety-tomentose. *Leaves* ovate to broadly ovate (12–)25–80(–110) × (20–)45–100(–180) mm or rarely oblong and 55–90 × 20–30 mm, sparsely pilose to tomentose with white silky trichomes above, pilose to velvety-tomentose below; leaf base cordate, subcordate or truncate occasionally shortly attenuate; apex acute with short acuminate tip or obtuse and abruptly contracted to acuminate tip; margin entire, rarely subentire to slightly crenate; lateral veins 6–10(–13) each side of midrib; upper pair of leaves at base of terminal inflorescence sessile, petiole (0–)8–80(–110) mm long, unwinged or lamina decurrent close to apex of petiole. *Inflorescence* a terminal, open, branching thyrse, 12.5–35 cm long,



Fig. 14 *Brillantaisia lamium* (Nees) Benth. A. Habit $\times 0.7$; B. Corolla dissection showing androecium $\times 2$; C. Gynoecium $\times 2$; D. Calyx $\times 2.5$; E. Capsule $\times 1.5$; F. Bract and bractlets $\times 1$.

often with smaller lateral panicles below, primary branches of inflorescence spreading almost at right angles to main axis, rachis usually sparsely covered in capitate glandular trichomes. *Bracts* ovate, adaxial surface pilose, often with slender multicellular trichomes, abaxial surface glabrous; bractlets rhomboid to linear, sessile, margin entire, adaxial surface covered with multicellular non-glandular trichomes, abaxial surface glabrous; becoming smaller and linear towards ends of lateral branches. *Sepals* sub-equal, linear, apex rounded, 4–7 mm long, green often tinged purplish; glabrous or with a few long glandular trichomes. *Corolla* deep bright blue-purple or violet occasionally pale lilac, one lip, often the upper; may be paler than the other; tube 5–8 × 2–4 mm, pale than lips, flushed inside with yellow, rarely completely white; upper lip (15–)22–30(–35) mm long, outer surface finely covered in glandular multicellular trichomes; lower lip (13–)19–27(–30) mm long, inner surface occasionally sparsely pubescent; apical lobe to 2 × 3 mm. *Androecium* with filaments 12–35 mm long, usually white; anthers 4.5–6 mm long; staminodes exerted for 4–5 mm from corolla tube, small vestigial anther. *Gynoecium* with style to 40 mm long, sparsely pubescent at base, stigma 3–5 mm long; ovary 3–4 mm long. Capsule 22–30 × (2–)3–5 mm with 14–16 seeds per locule, blunt tipped, green, tinged red at apex when immature, brown-black when mature and/or dried; glabrous or with a few erect, non-glandular trichomes at the apex, covered in black gland dots.

DISTRIBUTION. Throughout wet forest regions of west and central Africa, east to southern Sudan, through Zaire to northern Angola and through Uganda to northwest Tanzania.

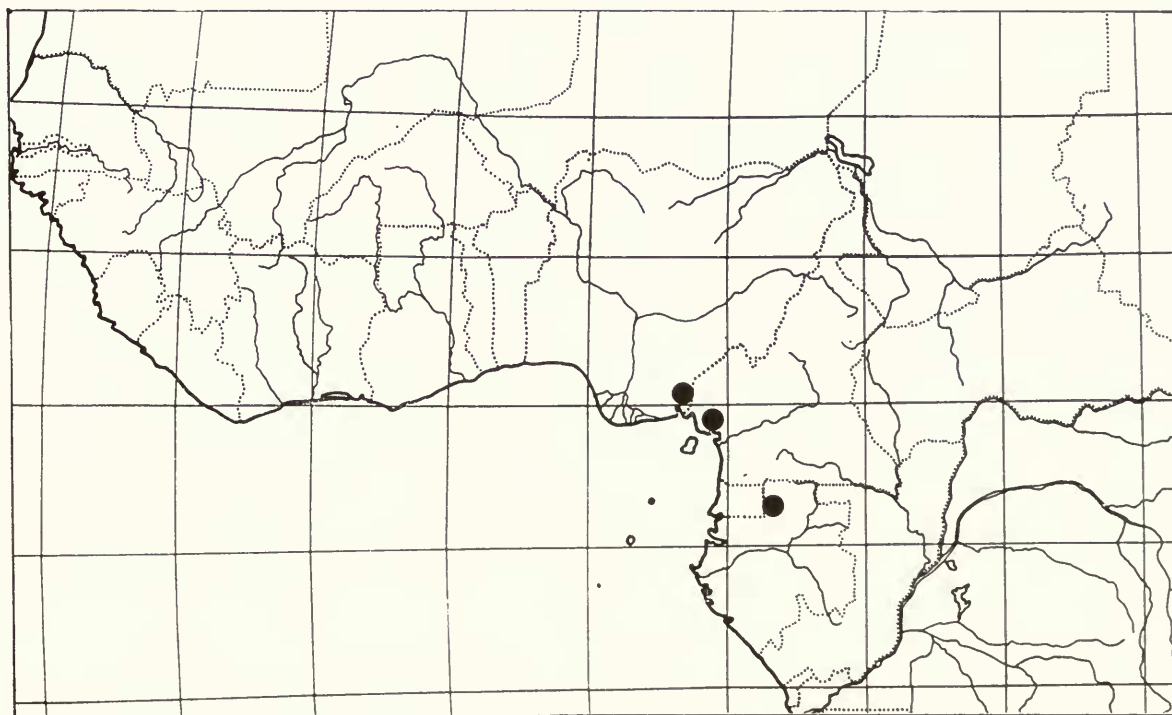
HABITAT. Forest clearings, shade beside rivers or streams, on lake shores or in swamps, often waterlogged/with roots in water, disturbed areas, roads, paths and plantations. In west Africa often very

weedy. 'In moist exposed woody situations almost everywhere' (on Princes Island, *Hiern*, 1900: 807). Common; 200–1600 m.

SELECTED COLLECTIONS

SIERRA LEONE: Njala, 30 October 1928, *Deighton* 1419 (BM, K, MO). LIBERIA: Louisiana, 11 November 1966, *Bos* 2310 (WAG); 10 miles N. of Monrovia, September 1970, *Jansen* 2207 (WAG). IVORY COAST: Sassandra, 18 June 1963, *de Wilde* 280 (K, WAG, Z); Foret de YAPO, 8 km S. of Becedi-Bugnan, 6 August 1963, *de Wilde* 641 (WAG); 27 October 1976, *Fabrigues* 3306 (P). GHANA: Banyimade, 10 September 1956, *Cudjoe*, 161 (WAG). TOGO: Kpandu, 1924, *Robertson* 62 (BM). NIGERIA: Oban, 1911, *Talbot* 981 (BM, K); Bauchi Plateau, August 1930, *Lely* 652 (MO); Cross River, 27 September 1985, *Gbile* 27 (MO). CAMEROON: Bibundi, October 1891, *Junger* 248 (UPS); Bipindi, 1896, *Zenker* 1104 (BM); NW of Tibati, 9 September 1963, *Letouzey* 5666 (P); Bakaka forest, 27 August 1971, *Leeuwenberg* 8206 (H, LISC, MO, UPS, WAG); Moundjo, 27 October 1975, *de Wilde* 8522 (WAG). BIOCCO: Malabo, near Baé Basula, 13 September 1986, *Carvalho* 2445, (BM); Sooyé, S. of Mamon, 16 February 1945, *Roberty* 6590 (G, Z). CENTRAL AFRICAN REPUBLIC: Koumbala, 25 October 1983, *Fay* 6055 (MO); Bambari, November 1923, *Tisserant* 1352 (P); *Tisserant* 3167 (BM, P). SÃO TOMÉ: 18 March 1968, *Espirito Santo* 4312 (LISC); Monte Cape, 14 August 1956, *Monod* 11681 (BM). DEMOCRATIC REPUBLIC OF THE CONGO: 26 June 1914, *Bequaert* 4836 (BR). BURUNDI: Ruyigi, 3 May 1980, *Reekmans* 9060 (MO, SRGH). SUDAN: Imatong mountains, Talanga, 2 December 1980, *Friis & Vollesen* 619 (C); Imatong Mountains, Acholi Hills, November 1981, *Howard* UTT 16 (C). ETHIOPIA: *Bidgood* s.n. (K). UGANDA: shores of Lake Nabugabo, 13 November 1934, *Taylor* 1660 (BM); Malabigambo forest, 15 August 1950, *Dawkins* D616 (BM). KENYA: Itare river, October 1940, *Copley* B1188 (G); Nairobi, 12 October 1972, *Hansen* 713 (C). ANGOLA: Loanda, 1903, *Gossweiler* 131 (BM).

Brillantaisia lamium is a widespread species that is readily recognized by the cordate leaves with an entire margin and unwinged petiole. The inflorescence is open and rather sparsely flowered with



Map 3 The distribution of *Brillantaisia lancifolia* Lindau.



Fig. 15 *Brillantaisia lancifolia* Lindau. A. Habit $\times 0.7$; B. Corolla dissection showing androecium $\times 2$; C. Gynoecium $\times 2$; D. Calyx $\times 2$; E. Bract and bractlets $\times 2$; F. Capsule $\times 2.2$.

few lateral branches that tend to be at right angles to the central axis. Fruit are characteristically glabrous but occasionally with a tuft of trichomes at the apex.

East African specimens of *Brillantaisia lamium* are often far more robust and pubescent than West African representatives, which tend to be slender herbs; however, the variation appears to be continuous and there are no morphological and/or geographical data to support subdivision of the species. Vollesen (in prep. a) notes 'A similar pattern where eastern plants from higher altitudes have larger flowers than western lowland plants is known from other Acanthaceae, e.g. *Albisepalum alboviolaceum*'. *Brillantaisia lamium* can form large weedy populations in areas of recently cleared vegetation or plantations of oil palm, cocoa or bananas, and in open grassy areas at higher altitude. In Cameroon slender low growing forms with very deep purple flowers were cultivated as an ornamental in small village compounds on Mount Cameroon. Collections from Kenya are of naturalized plants from Uganda and in swamp areas around Nairobi the species is now quite common.

9. ***Brillantaisia lancifolia*** Lindau in Engl. *Bot. Jahrb. Syst.* **17**: 98 (1893); Burkill in *Fl. trop. Afr.* **5**: 40 (1899); Benoist in *Bull. Soc. Bot. France* **60**: 335 (1913); Heine in *Fl. W. trop. Afr.* 2nd ed., **2**: 406 (1963); Heine in *Fl. Gabon* **13**: 86 (1966). Type: Gabon, Sierra del Crystal, Mann 1688 (B†-holotype, K!-lectotype, P!-isotype).

Fig. 15. Map 3.

B. talbotii S. Moore *Cat. pl. Talbot Oban distr.*: 75 (1913); Hutchinson & Dalziel in *Fl. W. trop. Afr.* **2**: 254 (1931). Type: S. Nigeria, Oban Talbot 2000 (BM!, K!-syntypes).

Icon: Heine, *Fl. Gabon*, Acanthacées: **13**: pl. 19 figs 1–3 (1966).

Perennial herb to 0.3–0.5 m tall. *Stems* 2–3 mm in diameter, glabrous to densely pubescent, petiole bases fused forming ridge across nodes. *Leaves* ovate-elliptic to lanceolate 25–130(–190) × 8–30(–50) mm, smaller on axillary shoots, glabrous or very sparsely pubescent; base cuneate; apex acute; margin entire to very shallowly serrated or crenate, subentire towards apex, entire towards base; main lateral veins 5–8 on each side; petiole 5–22 mm long, unwinged, lamina decurrent at apex. *Inflorescence* a delicate, open, few-flowered panicle 50–150 mm long, rachis glandular pubescent. *Bracts* often caducous, linear-lanceolate, bractlets if present linear lanceolate with rounded apex, sparsely pubescent. *Sepals* unequal, linear, tapering gradually towards the apex, larger upper sepal 6–10 mm long, smaller lateral sepals to 5–8 mm long, pubescent, with capitate glandular trichomes. *Corolla* deep blue to violet, often with brown marking in throat; corolla tube 5–10 × 2 mm, pale purple sometimes tinged green; upper lip 10–15(–20) × 2–3 mm, glandular pubescent, particularly of edge of upper lip; lower lip 10–18 × 6–8 mm, apical teeth rounded-triangular 1–2 × 1 mm. *Androecium* with filaments to 20 mm long, anthers 3–4 mm long; staminodes usually prominent, around half length of the corolla lips. *Gynoecium* with style 15–28 mm, stigma 1 mm, ovary 3 mm long, shortly glandular pubescent. *Capsule* 15 × 1–1.5 mm with c. 9–10 seeds per locule, brown when dry, evenly glandular pubescent.

DISTRIBUTION. Restricted to a few montane regions in Nigeria, Cameroon and Gabon.

HABITAT. On damp rocks, in dark ravines or at edges of waterfalls; 300–700 m.

SELECTED COLLECTIONS

NIGERIA: Oban, 1912, Talbot 2000 (BM, K). **CAMEROON:** Ebone-Yabassi, 27 December 1967, Bamps 1632 (BR); Mount Cameroon, above Batoke,

Thomas 2775 (MO). **GABON:** Cristal Mts, 21 January 1968, Halle & Villiers 4626 (P); Haute-Ngounye, 7 June 1926, Le Testu 5943 (BM, BR, P).

Very few specimens have been collected of *Brillantaisia lancifolia*. However, from available material and without further opportunity for field study, I maintain this species as clearly distinct from all other species of *Brillantaisia*. *Brillantaisia lancifolia* has lanceolate leaves unlike any other species in the genus, the plants tend to be delicate and leafy, with numerous axillary vegetative shoots. The nodes are regularly spaced and the internodes rarely exceed 40 mm. The inflorescence is also very delicate with few flowers. Few of the specimens studied have fruit and additional counts of seeds per locule are needed. Two collections from Cameroon (Leeuwenberg 8994, WAG; Hepper 1332, S) are intermediate in leaf shape between *B. lancifolia* and the less woody forms of *B. owariensis*; these specimens have ovate-elliptic leaves with a cuneate leaf base. However, the flowers on these specimens are far larger than those of typical *B. lancifolia* and have been provisionally determined as part of the large and variable *B. owariensis* group.

10. ***Brillantaisia debilis*** Burkill in *Fl. trop. Afr.* **5**: 39 (1899); Benoist in *Bull. Soc. Bot. France* **60**: 335 (1913). Type: Cameroon, Efulen, Batanga, Bates 350 (K!-lectotype, BM!, MO!, Z!-isotypes).

Fig. 16. Map 4.

Icon: Heine, *Fl. Gabon*, Acanthacées: **13**: pl. 16 figs 1–3 (1966).

B. soyauxii sensu Heine in *Fl. Gabon* **13**: 84, pl. 17, figs 1–3 (1966) non Lindau (1893); non Burkill (1899).

Leafy herbs 0.2–1 m tall. *Stems* 2–5 mm in diameter, often highly branched, rooting at nodes. *Leaves* elliptic-ovate to rhomboid, 45–110 × 25–58 mm, dull green, veins pale green to white; glabrous; lateral branches with smaller leaves 18–40 × 11–16 mm; leaf base cuneate; apex acuminate; margin entire to shallowly crenate; lateral veins 4–8 on each side of midrib; petiole 22–40(–80) mm, lamina decurrent towards base of petiole. *Inflorescence* a few flowered terminal panicle (50–)80–140(–180) mm long; rachis glabrous to glandular pubescent. *Bracts* ovate-obovate, 4–22 × 3–10 mm, rounded at apex; bractlets 1–5 mm long, narrowly oblong-obovate, glabrous to glandular pubescent, pedicel 1–2 mm long. *Sepals* subequal, linear, rounded at apex, 5–10 × 0.5–1 mm, pale green, fringed with unequal, purple, glandular trichomes. *Corolla* violet to deep bright purple with pale green or yellow spots in throat; tube 2–3 × 5–12 mm; upper lip 20–28 × 7–10 mm long, outer surface of upper lip covered in short entangled, glandular trichomes, more so at apex; lower lip 19–25 mm long, glabrous above, sparsely glandular pubescent below; apical lobes triangular to 2 × 2 mm. *Androecium* with filaments whitish to 20 mm long; anthers 3–4 mm long; staminodes 5 mm long, densely glandular with a small vestigial anther at apex. *Gynoecium* with style 25 mm long; stigma 2 mm long; ovary to 4 mm long, glabrous. *Capsule* 18–22 × 1–2 mm with 18–28 seeds per locule, brown, glabrous.

DISTRIBUTION. Cameroon and Gabon.

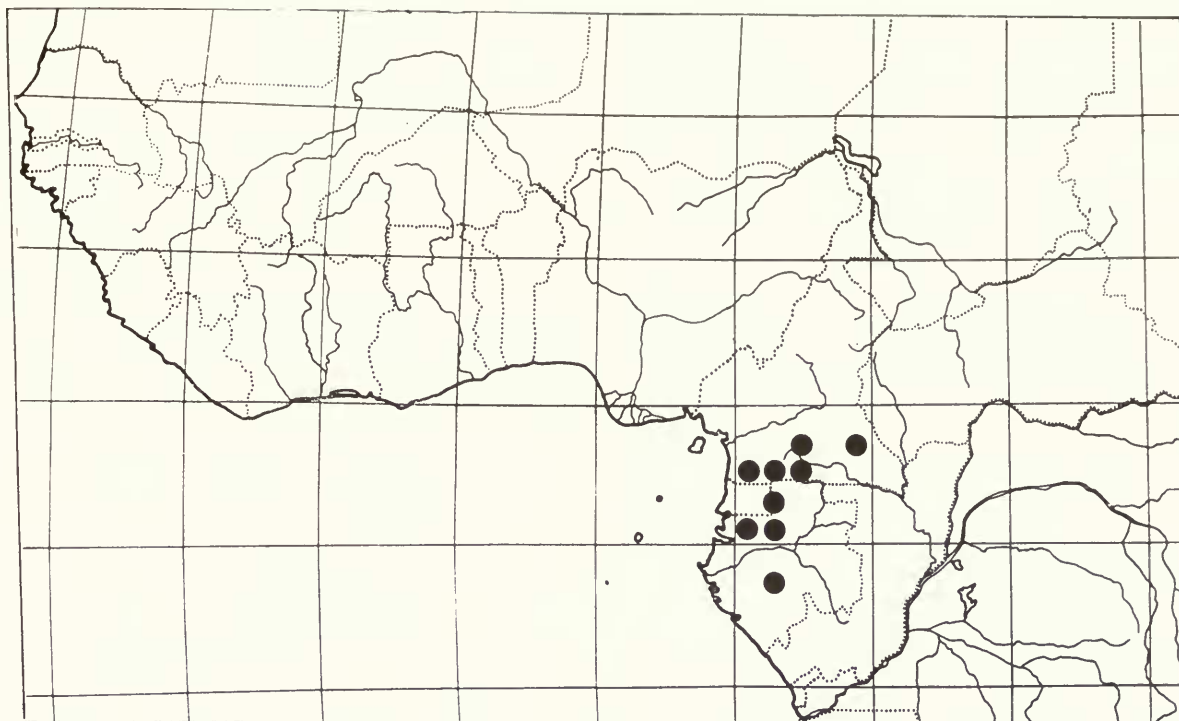
HABITAT. Along rivers in primary forest in rocky, mossy places. 400–500(–900) m.

SELECTED COLLECTIONS

CAMEROON: Yaounde, Bitye, Bates 1004 (BM, MO); Lolodorf, 1896, Staudt 240 (G. K. NY, S. WAG); Akoakas, 15 February 1963, Raynal & Raynal 9719 (P); near Molobo, 50 km S. of Batouri, 24 July 1963, Letouzey 5472 (P); Kwoinvom, 4 March 1964, de Wilde & de Wilde-Duyfjes 2072 (BR, MO, SRGH, WAG, Z); 3 km N. of Lomie, 8 September 1965, Leeuwenberg 6560 (LISC, MO, WAG); Nvem, near Bitye, 20 October 1967,



Fig. 16 *Brillantaisia debilis* Burkill. A. Habit $\times 0.7$; B. Corolla dissection showing androecium $\times 1.8$; C. Capsule $\times 2$; D. Gynoecium $\times 1.8$; E. Bract and bractlets $\times 1$.



Map 4 The distribution of *Brillantaisia debilis* Burkill.

Letouzey 8159 (P); 5 km E. of Meyo Centre, 24 March 1970, *Letouzey* 10229 (P); N'Koemvon, 11 October 1974, *de Wilde* 7635 (WAG); Rocher de Akoakas, 27 March 1981, *Meijer* 15307 (MO); Cult. WAG, 20 December 1985, *van der Laan* 986 (WAG). GABON: near lake Moudiboubacoudou, 6 April 1927, *Le Testu* 6478 (BM); *Le Testu* 9135 (BM); Monts de Cristal, 3 February 1968, *Halle & Villiers* 4897 (P); Akoga, 8 February 1968, *Halle & Villiers* 5047 (P); Cristal Mountains, 15 km NE of Asok, 21 August 1978, *Breteler & de Wilde* 187 (MO, WAG); Cristal Mountains, 21 January 1983, *de Wilde* et al. 133 (WAG); W. of Belinga, 18 July 1985, *Bos, van der Laan & Nzabi* 10696 (BR, WAG); 24 km SE of Medouneou, 5 February 1986, *Reitsma, Reitsma & Louis* 1880 (NY, WAG); Wolou-Ntem province, Chantier Oveng near Mitzic, 6 May 1986, *Louis* 2161 (WAG).

Plants of *Brillantaisia debilis* have few flowers and are often very leafy, the vegetative parts of plants of this species are entirely glabrous and the leaves are often purple underneath. The inflorescence may be glandular-pubescent on the rachis, peduncles, calyx and corolla. Many collections of this species have been mistakenly determined as *B. soyauxii*. In *Flore du Gabon*, Heine (1966) used the name *B. soyauxii* to describe a species which is glabrous except for the pedicels, calyx and, occasionally, the peduncles. The illustration of *B. soyauxii* in that work (Heine 1966: 87, 1–3) clearly fits the description of *B. debilis* given here. The type specimen of *B. soyauxii* has pubescent fruit, and a highly branched, many flowered inflorescence unlike *B. soyauxii* described in the *Flore du Gabon* (Heine 1966: 84–85) with few flowers and glabrous fruit. Other characters on the type specimen of *B. soyauxii* are inconsistent with the description of Heine (1966), including the larger, broader, spatulate upper calyx lobe and lower number of seeds in the fruit. *Soyaux* 454 is certainly a plant belonging to *B. vogeliana*.

11. ***Brillantaisia grottanellii*** Pichi-Sermoli in *Miss. Stud. Lago Tana 7. Recherche Botanique* 1: 254–255 (1951); Cufodontis, *Enum. pl. Aeth.*: 930 (1964). Type: Ethiopia, Tukur Dinghina forest, *Pichi-Sermoli* 2099 (FT-holotype, BM!-photo).

Map 5.

Erect aromatic herb to 1–2(–2.5) m tall. *Stems* 2–4 mm in diameter, rooting at nodes, covered in rather dense short, weak trichomes. *Leaves* ovate to broadly-ovate (35–)90–225(–250) × (10–)40–110(–150) mm, olive green to dull dark green above, paler below, glabrous to pubescent above and below; base cuneate; apex acuminate; margin crenate to serrate, occasionally serrulate; 8–13 veins each side of the midrib; petiole (10–)20–70(–110) mm, lamina decurrent along $\frac{1}{2}$ – $\frac{3}{4}$ length of petiole. *Inflorescence* a terminal spike (60–)80–200(–340) mm long with smaller lateral spikes below, flowers in distinct verticillate whorls, rachis often visible between verticillasters. *Bracts* ovate to linear-lanceolate, entire or crenate, rounded at apex, densely pubescent with glandular and eglandular trichomes, bractlets linear, trichomes as for bracts. Sepals subequal, linear rounded at apex, 0.5–1 × 12–20 mm, densely covered in long glandular and eglandular trichomes. *Corolla* dark blue-purple to violet or bright blue-lilac; tube 8–13 × (2–)3–5 mm; upper lip 20–30 × 4–6 mm covered in short glandular trichomes, which are slightly longer at the apex of the petals; lower lip 22–30 × 14–20 mm; apical lobes to 7 mm long, acute. *Androecium* with filaments 35–40 mm long; anthers 6–7 mm long; staminodes 5–10 mm long. *Gynoecium* with style 35 mm long pubescent to stigma, stigma 4 mm long. *Capsule* 20–22 × 2–3 mm with 8 seeds per locule, brown-black, covered with sparsely glandular trichomes.

DISTRIBUTION. Ethiopia and possibly Sudan.

HABITAT. Montane forest, beside streams in shade, in disturbed ground, occasionally collected from plantations; 1500–2000 m.

SELECTED COLLECTIONS

ETHIOPIA: Kaffa Prov., Beletta forest, 13 February 1957, *Mooney* 6725 (ETH); Wellega region near Dembidollo, Anfilo, 6 March 1957, *Mooney* 6890 (S); 7 km NW of Tippi airstrip, 14 January 1962, *Meyer* 7995 (US); 35 km W. of Lekemeti, 13 April 1966, *de Wilde & de Wilde-Duyffes* 10768 (MO, WAG); Kaffa Prov., Bonga, 9 January 1972, *Ash* 1454 (ETH, MO, UPS, WAG); Kaffa Prov., 57 km from Jimma on Sheki-Gogeb river track, 8

Table 5 Six characters which differ between plants of *Brillantaisia grottanellii* and *B. madagascariensis*.

Character	<i>B. grottanellii</i>	<i>B. madagascariensis</i>
Bract shape	lanceolate-ovate	broadly ovate-ovate
Glandular trichomes on bract	present	absent
Trichomes on style	along more than half length of style	at base of style only
Leaf margin	subentire-serrate	entire or crenate
Upper sepal shape	linear-spathulate	linear
Pollen ornamentation	smooth	irregularly spiny

December 1972. Friis et al. 1677 (C); Mt. Karkarha, 18 February 1976, Ash 3402 (MO, UPS); Gofa region, 10 km from Sawla, 27 December 1983 Ensermu & Zerihun 649 (C, ETH); 43 km from Mizan Teferi on road to Tepi, 27 January 1984, Ensermu et al. 745 (ETH); 37–41 km on the track from Gore to Masha, 1 February 1984, Ensermu et al. 821 (ETH); 27 km from Bebeke coffee plantation on road to Guraferda, 7 November 1985 Puff & Ensermu 861107-4/6 (ETH); Wellega Region, Bedelle/Arjo road–Didessa road crossing, 16 January 1990, Friis et al. 6023 (ETH); Kaffa Prov., Beletta forest, 18 January 1990, Friis et al. 6041 (ETH); SUDAN: Torit Distr., near Katire, 9 February 1950, Jackson 1144 (BM, MO), identity uncertain.

This species is clearly very closely related to *Brillantaisia madagascariensis* and, early in this study, was thought to be the same species. However, after detailed study of gross morphology and pollen characters, I recognize this species as distinct. Discussion with Dr Ensermu Kelbessa from Addis Ababa University who has studied these plants in the field convinces me that the *madagascariensis-grottanellii* group is best divided. Characters differentiating *B. grottanellii* from *B. madagascariensis* are shown in Table 5 and Figure 5.

12. ***Brillantaisia madagascariensis*** T. Anderson ex Lindau in *Bot. Jahrb. Syst.* **17**: 103 (1893); Burkill in *Fl. trop. Afr.* **5**: 43 (1899); Palacky, *Cat. pl. Madag.* **3**: 57 (1907); Chevalier, *Explor. bot. Afrique occ. franç.* **1**: 493 (1920); Hutchinson & Dalziel in *Fl. W. trop. Afr.* **2**: 254 (1931); Brenan & Greenway, *Checklist brit. empire 5 Tangan. Terr.* **2**: 5 (1949); Heine in *Fl. W. trop. Afr.* 2nd ed., **2**: 406 (1963); Cufodontis, *Enum. pl. Aeth.* 930 (1964); Benoist in *Fl. Madag. fam.* **182** **1**: 29 (1967); Agnew in *Upl. Kenya wild fls.* 583 (1974); Champluvier in *Fl. Rwanda* **3**: 446 (1985). Type: Madagascar, Betsileo, Nandihizana, Hildebrandt 3901 (B⁺-holotype; BM[!]-lectotype; G[!], M[!], P[!], W[!], Z[!]-isolectotypes).

Brillantaisia spicata Lindau in *Bot. Jahrb. Syst.* **20**: 4 (1894); in *Abh. Preuss. Akad. Wiss.* **50** & **54** (1894); in *Wiss. Erg. deut. Zentr.-Afr. Exped., Bot.* **2**: 293 (1911). Syntypes: Tanzania, Usambara Mountains, Bangarra Lutindi, Holst 3316 (COI, K[!]);

Usambara Mountains, Gonja, Handei, Holst 4216 (COI, G[!], K[!], M[!], P[!], W[!], WAG[!], US[!], Z[!]).

B. verruculosa Lindau in *Bot. Jahrb. Syst.* **22**: 113 (1897); Burkill in *Fl. trop. Afr.* **5**: 43 (1899); Mildbraed, *Wiss. Erg. zweit. deut. Zentr.-Afr. Exped., Bot.*: 192 (1922); Robyns *Fl. parc. nat. Albert* **2**: 269 (1947); Heine in *Fl. Gabon* **13**: 89 (1966). Type: Cameroon, Yaounde, Zenker & Staudt 166 (B⁺-holotype).

B. bagshawei S. Moore in *J. Bot.* **46**: 312–313 (1908). Type: Uganda, Bugoma forest, Bagshawe 1387 (BM[!]-holotype).

B. majestica Wernham in *J. Bot.* **54**: 229 (1969). Type: Cameroon, Buea, Mount Cameroon, Bates 817 (K[!]-holotype).

Icones: Heine, *Fl. Gabon*, Acanthacées: **13**: pl. 18 figs 7–15 (1966); Benoist in *Fl. Madag. fam.* **182**, Acanthacées: fig. IV 8–13 (1967).

Erect or scrambling much branched herb 0.2–2 m tall. *Stems* 2–5(–8) mm in diameter, shortly pubescent, more densely so at nodes, glabrous below. *Leaves* ovate to broadly ovate, 40–150(–180) × 30–90(–130) mm, lower leaves becoming much larger, to 400 × 500 mm, usually sparsely pubescent, with short white or translucent trichomes on midrib and main veins, occasionally densely pilose; leaf base attenuate, occasionally truncate or cordate; apex acute-acuminate; margin entire, occasionally slightly crenate; 8–12(–14) main lateral veins each side of midrib; petiole 6–90 mm long, winged for 2/3 of length. *Inflorescence* a terminal spike with smaller lateral spikes below (20–)40–220(–350) mm long, flowers crowded into dense verticillate whorls, rachis densely pubescent, not usually visible between verticillasters. *Bracts* ovate to elliptic, apex rounded to acuminate, green with purple tinge, persistent. *Sepals* subequal, slender tapering to apex or linear and rounded at the apex, occasionally spatulate, larger upper sepal 10–30 × 1–2 mm, very slightly longer than the other four; lateral sepals 8–25 × 1–2 mm; green, red to purple at apex, densely pubescent on abaxial surface, trichomes white, less dense shorter trichomes on adaxial surface. *Corolla* variable shades of blue-purple, violet, magenta or white, with lateral yellow spots in the throat; corolla tube to 15 mm long; upper lip 15–30 × 5–8 mm, glandular pubescent outside occasionally with long trichomes; lower lip 15–25 × 10–12 mm, apical lobes 2–5 × 2–3 mm,

often short, rounded-blunt but can be longer, narrowly triangular with acute apex. *Androecium* with filaments 20–22 mm long, white; anthers 3–6(–8) mm long, creamy yellow or brown, pubescent along one side; staminodes 5–10 mm long. *Gynoecium* with style 25 mm long, often persistent when corolla has fallen, stigma 2.5 mm long; ovary 3–5 mm long. *Capsule* 18–30 × 3–5 mm with 6–8 seeds per locule, black-brown, glandular puberulous with longer scattered eglandular trichomes.

DISTRIBUTION. Throughout West Africa through the Congo basin to Ethiopia and south into Tanzania, also in Madagascar.

HABITAT. Montane forest, often weedy in plantations, recently logged areas, clearings or pathsides; 500–1200 m.

SELECTED COLLECTIONS

LIBERIA: Yéképa, Yiti village, 24 January 1965, *Adam* 20734 (K, MO). BIOCCO: November 1911, *Mildbraed* 7126 (H). CAMEROON: 2°00'N 12°15'E, 2 January 1911, *Mildbraed* 4147 (H). GABON: Haute-Ngounyé, 1924–1927, *Le Testu* 6431 (BM, MO); Lastoursville region, 1929–1931, *Le Testu* 8853 (BM, P). RWANDA: Nyungwe forest, near Rukuzi, 4 May 1972, *Bouxin* 1577 (BR). BURUNDI: Mabaya-Hua on Rwandan border, 22 June 1969 *Lewalle* 3783 (BR, G, SRGH); Mabayi valley, Bubanza, 16 October 1971, *Reekmans* 1136 (BR). SUDAN: Torit District, Lotti forest, 2 January 1950, *Jackson* 1023 (BM); Talanga, 1 December 1980, *Friis & Vollesen* 613 (C). ETHIOPIA: Kaffa Prov., Abetu valley, near Belita, 18 October 1954, *Mooney* 6071 (ETH, K, S); 10 km E. of Bonga along Jimma road, 22 December 1965, *de Wilde* 9415 (C, DSM, ETH, MO, UPS, WAG); Kaffa Prov., Bonga, 20 November 1970, *Friis, Hounde & Jacobsen* 369 (C); Illubabor Prov., 22 km S. of Gore, 19 December 1972, *Friis et al.* 1882 (C). UGANDA: Budongo Forest, 7 February 1935, *Taylor* 3327 (BM, MO); Mabira Forest, 8 November 1938, *Loveridge* 26 (MO). DEMOCRATIC REPUBLIC OF THE CONGO: Kasongo-Kindu road, km 60, 29 June 1952, *Germain* 7826 (PRE); Valley de la Mbizi, near Burora, 10 May 1957, *Gutzwiller* 841 (BR); Kivu, W. of Kaluzi Mts, 26 April 1978,

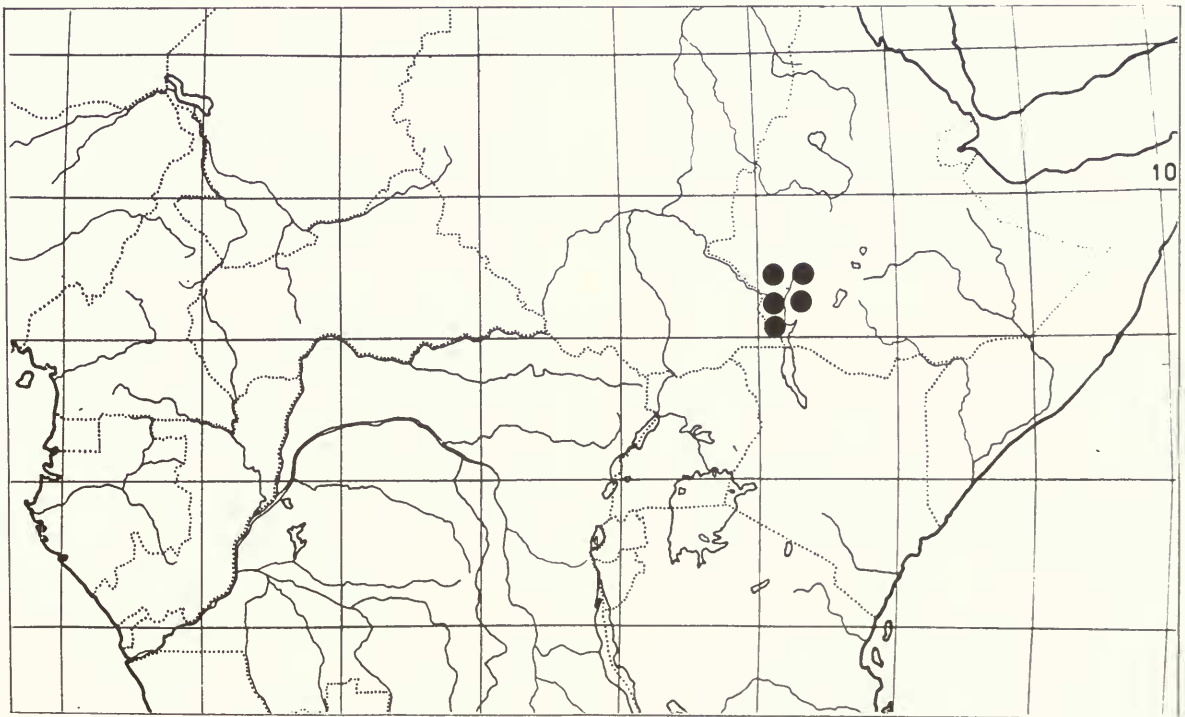
Lambinon 78/321 (BR). KENYA: Kakamega forest, 17 November 1975, *Cunningham* s.n. (LISC). TANZANIA: Mt Meru, Surra Forest, 10 November 1969, *Richards* 24663 (C, M); Mshituni, above tea estate N. of Derema, 5 October 1979, *Kibuwa* 5191 (UPS). MADAGASCAR: August 1902, *Perrier* 9227 (P); near Doanyanala, 25 January–25 February 1949, *Humbert* 23090 (P); 6 December 1963, *Rakotozafy* 287 (P).

Plants of this species are very distinctive in flower and fruit, with a narrowly spicate inflorescence, flowers in verticillasters, persistent bracts and linear, pubescent calyx lobes. *Brillantaisia verruculosa* has been upheld as a species by several recent workers, notably Heine (1966), solely on the basis of the floral colour being white rather than purple. White flowers are found in three other species of *Brillantaisia* and as this is the only character on which Heine split *B. madagascariensis*, I maintain this variation under the earliest name.

NOMEN DUBIUM

Brillantaisia cicatricosa Lindau in *Bot. Jahrb. Syst.* **20**: 4 (1895) nomen dubium; Lindau in *Pflanzenw. Ost-Afr.* **C**: 366 (1895); Burkill in *Fl. trop. Afr.* **5**:39 (1899); Mildbraed, *Deutsch Zent. Afr. Exped.* (1922); Robyns, *Fl. parc. nat. Albert* **2**: 270 (1947); Troupin, *Fl. pl. lign. Rwanda*: 84 (1982); Champluvier in *Fl. Rwanda* **3**: 446 (1985); Fischer & Hinkel, *Nat. Env. Rwanda*: 81, fig. 68 (1992). Type: Zaire, W. slope of Ruwenzori Mountains, Buhtahu Valley, *Stuhlmann* 2301 (B⁺-holotype). Problems with the application of this name are described in detail above (p. 95).

Brillantaisia hirsuta T. Anderson in *Journ. Agric.-Hort. Soc. NS* **1**: 267 (1868). This name refers to a plant introduced to the Royal Botanic Gardens, Calcutta from Kew and which cannot now be traced. Anderson wrote of this species that 'It is common on the



Map 5 The distribution of *Brillantaisia grottanellii* Pichi-Sermoli.

banks of streams in Western equatorial Africa. It differs from *B. owariensis* in its very prostrate habit, much smaller non decurrent leaves and in the smaller size of its flowers which are not glandular'. This description may refer to *Brillantaisia vogeliana* which has sparsely pubescent flowers, however, as this is the only information regarding the the identity of the plant in Calcutta, application of this name remains uncertain.

Species transferred to *Hygrophila*

Brillantaisia borellii Lindau in *Bot. Jahrb. Syst.* **33**: 186 (1904). This species was considered to be very different from all other *Brillantaisia* species due to the presence of four fertile stamens, very narrow leaves and the lack of an upper corolla lip.

Brillantaisia didynama Lindau in *Bot. Jahrb. Syst.* **24**: 313 (1898). Considered by Lindau to be clearly distinct from all other species of *Brillantaisia* by virtue of having four fertile stamens and very distinctive pollen, Lindau maintained this species within the genus and placed it close to *B. lancifolia* due to the few-flowered inflorescence and lanceolate leaves.

Brillantaisia thwaitesii Cramer in *Kew Bull.* **46**: 335–338 (1991). Cramer transferred *Plaesianthera thwaitesii* (C.B. Clarke) Livera to *Brillantaisia* as he considered it close to *Brillantaisia pubescens*. Recent studies (Sidwell, in press *a*) have shown that the species is best placed in *Hygrophila* until a greatly needed monograph of that genus is undertaken.

Species transferred to *Eremomastax*

Brillantaisia fulva Lindau in *Bot. Jahrb. Syst.* **24**: 313–314 (1898).

ACKNOWLEDGEMENTS. I would like to thank Robert Scotland and Kaj Vollesen for supervision throughout the course of my PhD study. Thanks also to John Baker, Ian Gourlay, Julie Hawkins, David Mabberley, Alison Strugnell and Rosemary Wise in Oxford; Alex Ball and Louisa Jones in the SEM unit at The Natural History Museum; everyone at Limbe Botanic Gardens and the National herbarium in Cameroon; Martin Cheek and Alan Paton at Kew and Axel Poulsen in Copenhagen. This research was funded by BBSRC research grant 93309762, with additional financial assistance from Wolfson College Oxford and the University of Oxford Hardship Fund. Funding to cover materials and tuition for all illustrations was received, with thanks, from the Linnean Society of London's A.G. Side fund for research in systematic biology.

REFERENCES

- Ahmad, K.J. 1976. Epidermal studies in some species of *Hygrophila* and *Dyschoriste* (Acanthaceae). *Journal of the Indian Botanical Society* **55**: 41–52.
- 1978. Epidermal hairs of Acanthaceae. *Blumea* **24**: 101–117.
- Anderson, T. 1875. *Brillantaisia alata* and *Brillantaisia pubescens*, In D. Oliver (Ed.), The Botany of the Speke and Grant Expedition. *Transactions of the Linnean Society of London* **29**: 125–126.
- Baden, C. 1981. The genus *Anisotes* (Acanthaceae): a taxonomic revision. *Nordic Journal of Botany* **1**: 623–664.
- Baillon, H. 1891. Acanthacées. In H. Baillon, *Histoire des plantes*: **10**: 403–466. Paris.
- Balkwill, K. & Getliffe-Norris, F. 1985. Taxonomic studies in the Acanthaceae; the genus *Hypoestes* in southern Africa. *South African Journal of Botany* **51**: 133–144.
- Getliffe-Norris, F. & Balkwill, M.-J. 1996. Systematic studies in the Acanthaceae; *Dicliptera* in southern Africa. *Kew Bulletin* **51**: 1–61.
- Bateman, R.M., DiMichele, W.A. & Willard, D.A. 1992. Experimental cladistic analysis of anatomically preserved arborescent lycopsids from the carboniferous of Euramerica: an essay on palaeobotanical phylogenetics. *Annals of the Missouri Botanical Garden* **79**: 500–559.
- Benoist, R. 1967. Acanthacées. In H. Humbert (Ed.), *Flore de Madagascar et des Comores*: 182^e famille. Paris.
- Benthams, G. 1849. *Brillantaisia*. In W. J. Hooker, (Ed.) *Niger Flora*: 477–478. London.
- 1876. Acanthaceae. In G. Benthams, & W. J. Hooker (Eds), *Genera plantarum*: **2**: 1060–1122. London.
- Blackmore, S. & Tootill, E. (Eds) 1984. *The Penguin dictionary of botany*. Middlesex.
- Bremekamp, C.E.B. 1944. Materials for a monograph of the Stobilanthinae (Acanthaceae). *Verhandelingen der Nederlandse Akademie van Wetenschappen Afdeling Natuurkunde* **41**: 1–305.
- 1953. The delimitation of the Acanthaceae. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen* **56**: 533–546.
- 1965. Delimitation and subdivision of the Acanthaceae. *Bulletin of the Botanical Survey of India* **7**: 21–30.
- Burkill, L.H. 1899. *Brillantaisia*. In W.T. Thistleton-Dyer, (Ed.), *Flora of Tropical Africa*: **5**: 37. London.
- Carlquist, S. & Zona, S. 1988. Wood anatomy of Acanthaceae: a survey. *Aliso* **12**: 201–227.
- Champluvier, D. 1985. *Brillantaisia*. In G. Troupin, (Ed.) *Flore du Rwanda: Spermatophytes* **3**: 444–448. Tervuren.
- Chappill, J.A. 1989. Quantitative characters in phylogenetic analysis. *Cladistics* **5**: 217–234.
- Cramer, L.H. 1991. *Brillantaisia* P. Beauv. (Acanthaceae), a new generic record for Asia. *Kew Bulletin* **46**: 335–338.
- Cranston, P.S. & Humphries, C.J. 1988. Cladistics and computers: a chironomid conundrum? *Cladistics* **4**: 72–92.
- Daniel T.F. 1984. Revision of *Stenandrium* (Acanthaceae) in Mexico and adjacent regions. *Annals of the Missouri Botanical Garden* **71**: 1028–1043.
- De, A. 1960. Cytological, anatomical and palynological studies as an aid in tracing affinity and phylogeny in the family Acanthaceae. IV. *Transactions of the Bose Research Institute Calcutta* **31**: 17–29.
- De Pinna, M.C.C. 1996. Comparative biology and systematics, some controversies in retrospective. *Journal of Comparative Biology* **1**: 3–16.
- Doyle, J.A. & Donoghue, M.J. 1986. Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. *The Botanical Review* **52**: 321–431.
- Ensermu, K. 1990. *Justicia sect. Ansellia* (Acanthaceae). *Acta Universitatis Upsaliensis Symbolae Botanicae Upsaliensis* **29**: 1–96.
- Erdtman, G. 1960. The acetolysis method. A revised description. *Svensk Botanisk Tidskrift* **54**: 561–564.
- Exell, A.W. 1944. *Catalogue of the vascular plants of S. Tomé (with Principe and Annobon)*. London.
- Ezcurra, C. 1993. Systematics of *Ruellia* (Acanthaceae) in southern south America. *Annals of the Missouri Botanical Garden* **80**: 787–845.
- Farris, J.S. 1988. *Hennig86: version 1.5*. Published by the author, Jamaica Plains.
- Furness, C.A. 1994. The pollen morphology of *Hygrophila* and *Brillantaisia* (Acanthaceae: Ruellieae). *Acta Botanica Gallica* **141**: 267–278.
- Gift, N. & Stevens, P.F. 1997. Vagaries in the delimitation of character states in quantitative variation – an experimental study. *Systematic Botany* **46**: 112–125.
- Graham, V.A.W. 1988. Delimitation and infra-generic classification of *Justicia* (Acanthaceae). *Kew Bulletin* **43**: 551–624.
- Grubert, M. 1974. Studies on the distribution of myxospermy among seeds and fruits of angiospermae and its ecological importance. *Acta Biologica Venezuela* **8**: 315–551.
- Hauser, D.L. & Presch, W. 1991. The effect of ordered characters on phylogenetic reconstruction. *Cladistics* **7**: 243–265.
- Hedrn, M. 1989. *Justicia* sect. *Harnieria* (Acanthaceae) in tropical Africa. *Acta Universitatis Upsaliensis Symbolae Botanicae Upsaliensis* **29**: 1–141.
- Heine, H. 1966. Acanthacées. In A. Aubreville (Ed.), *Flore du Gabon*: **13**. Paris.
- Hennig, W. 1950. *Grundzüge einer Theorie der Phylogenetischen Systematik*. Berlin.
- 1979. *Phylogenetic systematics*. Translated by D. D. Davis & R. Zangerl. Chicago.
- Hiern, W.P. 1900. *Catalogue of the African plants collected by Dr Friedrich Welwitsch in 1853–1861*. London.
- Hobcin, M. 1884. Über den systematischen werth der cystolithen bei den Acanthaceen. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **5**: 422–440.
- Holmgren, P.K., Holmgren, N.H. & Barnett, L.C. 1990. *Index Herbariorum*. New York.
- Hooker, W.J. 1853. *Brillantaisia owariensis* P. Beauv. *Curtis's Botanical Magazine*. **79**: t.4717.
- Immelman, K.L. 1989. Studies in the southern African species of *Justicia* and *Siphonoglossa* (Acanthaceae): palynology. *Bothalia* **19**: 151–156.
- 1990. Studies in the southern African species of *Justicia* and *Siphonoglossa* (Acanthaceae): seeds. *Bothalia* **21**: 49–59.
- Inamdar, J.A., Chaudhari, G.S. & Ramana Rao, T.V. 1990. Studies on the cystoliths of Acanthaceae. *Feddes Repertorium* **101**: 417–424.

- Kippist, R.** 1845. On the existence of spiral cells in the seeds of Acanthaceae. *Transactions of the Linnean Society of London* **19**: 65–76.
- Lester, R.N. & Ezcurra, C.** 1991. Enzyme etching treatment as an aid in the study of seed surface sculpture in *Justicia* and *Ruellia* (Acanthaceae). *Botanical Journal of the Linnean Society* **105**: 285–288.
- Lindau, G.** 1893. Acanthaceae Africanae 1. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **17**: 89–113.
- 1894. Beiträge zur systematik der Acanthaceen. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **18**: 36–64.
- 1895a. Acanthaceae. In A. Engler & K. Prantl (Eds), *Die Natürlichen Pflanzenfamilien*: **4(3b)**: 274–354. Leipzig.
- 1895b. *Brillantaisia anomala* and *B. cicatricosa*. In A. Engler (Ed.), *Die Pflanzenwelt Ost-Afrikas und der Nachbargebiete*. Geographische Verlagshandlung: 366. Berlin.
- 1895c. Acanthaceae Africanae 2. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **20**: 1–76.
- 1895d. *Brillantaisia ulugurica*. In A. Engler (Ed.), *Die Pflanzenwelt Ost-Afrikas und der Nachbargebiete*. Geographische Verlagshandlung: 91. Berlin.
- 1896. *Brillantaisia kirungae*. In G. A. von Götzen (Ed.), *Verzeichniss der auf der Graf. v. Götzen'schen Expedition bei der Besteigung des Kirunga gesammelten pflanzen*: 9.
- 1897. Acanthaceae Africanae 3. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **22**: 112–127.
- 1898. Acanthaceae Africanae 4. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **24**: 310–325.
- 1904. Acanthaceae Africanae 6. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **33**: 183–193.
- Lindley, J.** 1847. *The vegetable kingdom*. London.
- 1853. Notices of new or rare garden plants. *Journal of the Horticultural Society of London* **8**: 128–130.
- Luckow, M.** 1995. Species concepts: assumptions, methods and applications. *Systematic Botany* **20**: 589–605.
- Mabberley, D.J.** 1987. *The plant book*. Cambridge.
- McDade, L.A.** 1995. Species concepts and problems in practice: insight from botanical monographs. *Systematic Botany* **20**: 606–622.
- Maddison, W.P.** 1993. Missing data versus missing characters in phylogenetic analysis. *Systematic Biology* **42**: 576–581.
- Manktelow, M.** 1996. *Phaulopsis* (Acanthaceae) – a monograph. *Acta Universitatis Upsaliensis Symbolae Botanicae Upsaliensis* **31**: 1–184.
- Manning, J.C. & Getliffe-Norris, F.** 1985. Taxonomic studies in the Acanthaceae: A reappraisal of the genera *Duvernoia* and *Adhatoda* in southern Africa. *South African Journal of Botany* **51**: 475–484.
- Mayr, E.** 1942. *Systematics and the origin of species*. New York.
- Mickevich, M.F. & Lipscomb, D.** 1991. Parsimony and the choice between different transformations for the same character set. *Cladistics* **7**: 111–139.
- Mildbraed, J.** 1946. *Brillantaisia cicatricosa* Lindau var. *kivuwensis* Mildbraed var. nov. *Bulletin du Jardin Botanique de l'Etat* **17**: 86.
- Nees von Esenbeck, C.G.** 1832. Acanthaceae. In N. Wallich (Ed.), *Plantae Asiaticae Rariores*: **3**. London.
- 1847. Acanthaceae. In A. de Candolle (Ed.), *Prodromus Systematis Naturalis Regni Vegetabilis*: **11**: 46–519. Paris.
- Nelson, G.J. & Platnick, N.I.** 1981. *Systematics and biogeography: cladistics and vicariance*. New York.
- Nixon, K.C.** 1992. *CLADOS: version 1.38.1*. New York.
- & **Davis, J.I.** 1991. Polymorphic taxa, missing values and cladistic analysis. *Cladistics* **7**: 233–241.
- & **Wheeler, Q.D.** 1990. An amplification of the phylogenetic species concept. *Cladistics* **6**: 211–223.
- Palisot de Beauvois, A.M.F.J.** 1818. *Flore d'Oware et de Benin en Afrique*. 67–68. t.100. Paris.
- Pimentel, R.A. & Riggins, R.** 1987. The nature of cladistic data. *Cladistics* **3**: 201–209.
- Platnick, N.I., Griswold, C.E. & Coddington, J.A.** 1991. On missing entries in cladistic analysis. *Cladistics* **7**: 337–343.
- Pleijel, F.** 1995. On character coding for phylogeny reconstruction. *Cladistics* **11**: 309–315.
- Punt, W., Blackmore, S., Nilsson, S. & Le Thomas, A.** 1994. Glossary of pollen and spore terminology. *LPP Contributions series No.1*. Utrecht.
- Quicke, D.L.J.** 1993. *Principles and techniques of contemporary taxonomy*. London.
- Radlkofer, L.** 1883. Ueber die systematischen Werth der Pollenbeschaffenheit bei den Acanthaceen. *S. B. bayer. Akademie der Wissenschaften., math-phys. Cl.* **13**: 256–314.
- Raj, B.** 1961. Pollen morphological studies in the Acanthaceae. *Grana Palynologica* **3**: 1–108.
- Ramos, T.** 1997. *Tree Gardener: version 2.2*. São Paulo.
- Rickett, H.W.** 1944. The classification of inflorescences. *Botanical Review* **10**: 187–231.
- 1955. Materials for a dictionary of botanical terms—III, Inflorescences. *Bulletin of the Torrey Botanical Club* **82**: 419–445.
- Schaffnit, E.** 1906. Beiträge zur anatomie der Acanthaccen-samen. *Beiliefte zum Botanischen Zentralblatt* **19**: 453–484.
- Scotland, R.W.** 1991. A systematic analysis of Acanthaceae genera with contorted corollas. In S. Blackmore & S.H. Barnes (Eds), *Pollen and Spores, Patterns of Diversification*: Systematics Association special volume No. **44**: 269–289. Oxford.
- 1992a. Pollen morphology and taxonomic characters in Acanthaceae. *Systematic Botany* **17**: 337–340.
- 1992b. Systematics, similarity and Acanthaceae pollen morphology. *Botanical Journal of the Linnean Society* **109**: 529–541.
- 1992c. Chapter 2 – Character coding. In P.L. Forey, C.J. Humphries, I.J. Kitching, R.W. Scotland, D.J. Siebert & D.W. Williams (Eds), *Cladistics: A Practical Course in Systematics*: Systematics Association Publication No. **10**: 14–21. Oxford.
- 1993. Pollen morphology of Contortae (Acanthaceae). *Botanical Journal of the Linnean Society* **111**: 471–504.
- **Endress, P.K., & Lawrence, T.J.** 1994. Corolla ontogeny and aestivation in the Acanthaceae. *Botanical Journal of the Linnean Society* **114**: 49–65.
- **Sweere, J.A., Reeves, P.A. & Olmstead, R.G.** 1995. Higher-level systematics of Acanthaceae determined by chloroplast DNA sequences. *American Journal of Botany* **82**: 266–275.
- Sell, Y.** 1969a. Les complexes inflorescentiels de quelques Acanthacées étude particulière des phénomènes de condensation, de racemisation d'homogénéisation et de truncature. *Annales des Sciences Naturelles Botanique, Paris Séries 12* **10**: 225–300.
- 1969b. La dissémination des Acanthacées: Variations sur le type xérochasique fondamental. *Revue Générale Botanique* **76**: 417–453.
- Selvaraj, R. & Subramanian, D.** 1983. Epidermal studies in some species of Acanthaceae. *Journal of the Indian Botanical Society* **62**: 253–258.
- Sidwell, K.J.** 1997. A revision of *Brillantaisia* P. Beauv. (Acanthaceae). Unpublished PhD. thesis. University of Oxford.
- In press a. The taxonomic position of the anomalous Sri Lankan species *Brillantaisia thwaitesii* (T. Anderson) Cramer (Acanthaceae) from Sri Lanka. *Kew Bulletin*.
- In press b. Monographing *Brillantaisia* P. Beauv. (Acanthaceae): How to delimit species and higher taxa? *Proceedings of the 15th AETFAT Congress*. Harare.
- Singh, V. & Jain, D.K.** 1975. Trichomes in Acanthaceae 1: General structure. *Journal of the Indian Botanical Society* **54**: 116–127.
- Stevens, P.F.** 1984. Homology and phylogeny, morphology and systematics. *Systematic Botany* **9**: 395–409.
- 1991. Character states, morphological variation and phylogenetic analysis: a review. *Systematic Botany* **16**: 553–583.
- Thiele, K.** 1993. The holy grail of the perfect character: the cladistic treatment of morphometric data. *Cladistics* **9**: 275–340.
- Troll, W.** 1964. *Die Inflorescenzen: Typologie und Stellung im Aufbau des Vegetationskörpers 1*. Stuttgart.
- Vollesen, K.** In prep a. Acanthaceae. *The Flora of Tropical East Africa*.
- In prep b. Acanthaceae. *Flora Zambesiaca*.
- & **Brummitt, R.K.** 1981. Notes on *Brillantaisia pubescens* (Acanthaceae) with particular reference to discontinuity in flower size. *Kew Bulletin* **36**: 569–573.
- Weberling, F.** 1989. *Morphology of flowers and inflorescences*. Cambridge.
- White, F.** 1962. Geographic variation and speciation in Africa with particular reference to *Diospyros*. In D. Nichols (Ed.), *Taxonomy and geography*: Systematics Association Publication No. **4**: 71–103. London.
- 1984 *Unpublished fieldnotes*. Department of Plant Sciences, University of Oxford.
- Wilkinson, M.** 1995. A comparison of two methods of character construction. *Cladistics* **11**: 297–308.
- Wood, J.R.I.** 1995. Notes on *Strobilanthes* (Acanthaceae) for the flora of Ceylon. *Kew Bulletin* **50**: 1–24.

EXSICCATAE

Abdallah & Vollesen 95/176. pubescens (K).

Achien 524. lamium (BR).

Adam 2968. owariensis (K. MO); 4782. *lamium* (BR. K); 4830. *lamium* (MO); 5286. *lamium* (MO); 6910. *lamium* (MO); 7351. *lamium* (MO); 16325. *lamium* (K. P); 16453. *lamium* (K); 20464. *lamium* (K); 20549. *owariensis* (BR. K, MO, P. UPS); 20734. *madagascariensis* (K, MO); 22019. *owariensis* (MO. P); 22262. *lamium* (MO); 22916. *owariensis* (MO, P); 23291. *lamium* (MO, PRE); 24116. *lamium* (MO); 24302. *lamium* (MO); 24663. *lamium* (MO); 24795. *lamium* (MO, PRE); 25258. *owariensis* (MO); 26520. *lamium* (MO); 26558. *lamium* (MO, PRE); 27084. *owariensis* (MO); 30140. *lamium* (MO).

Adames 73. lamium (K); 694. *lamium* (K); 791. *owariensis* (K. UPS).

Adebusnyi FHI 43972. lamium (K).

Afzelius s.n., lamium (UPS).

- Ake Assi* 3244, *lamium* (G); 3333, *owariensis* (G); 5502, *owariensis* (G); 7186, *lamium* (G); 9136, *vogeliana* (G); 9243, *lamium* (G); 12211, *owariensis* (G, Z); 15745, *lamium* (G); 17170, *owariensis* (G).
Alluard 309, *owariensis* (P); 390, *owariensis* (P).
Anderson 1383, *lamium* (K).
Andrada 1811, *kirungae* (LISC).
Ansell 1842, *lamium* (K).
Arclibold 2589, *kirungae* (C).
Arends & Groenendijk 3, *vogeliana* (WAG); 95, *vogeliana* (WAG).
Ariwaodo 33, *owariensis* (MO); 77, *owariensis* (MO).
Asl 1454, *grottanellii* (ETH, MO, UPS, WAG); 3402, *grottanellii* (MO, UPS).
Auquier 2684, *owariensis* (BR).
Babault s.n. *owariensis* (P); s.n. *kirungae* (P).
Bagslawe 1131, *owariensis* (BM); 1270, *kirungae* (US); 1342, *owariensis* (BM); 1381, *madagascariensis* (BM); 1506, *owariensis* (BM).
Baldwin 10182, *owariensis* (K, MO); 10778, *owariensis* (K, MO); 5993, *lamium* (K, MO); 6175, *lamium* (K); 6339, *lamium* (K); 7070, *lamium* (K, MO).
Ball 62, *kirungae* (MAL, SRGH).
Banps 1632, *lanceifolia* (BR); 2592, *lamium* (K).
Banda & Kaunda 3452, *riparia* (MO).
Banda & Salubeni 1571, *riparia* (MO, SRGH).
Barbosa 1812, *riparia* (LISC); 2042, *pubescens* (LISC); 2395, *pubescens* (LISC).
Barker 1131, *lamium* (K); 1418, *lamium* (K).
Barton (?) 103, *lamium* (K).
Bates 216, *vogeliana* (BM, E, K, G, Z); 350, *debilis* (BM, K, MO, Z); 435, *owariensis* (BM); 1004, *debilis* (BM, MO).
Batten-Poole 209, *owariensis* (K).
Bauer 175, *vogeliana* (K).
Baumann 67, *lamium* (K).
Bayliss s.n. *owariensis* (MO).
Beddome s.n. *lamium* (K).
Beguïn & Gautier 266, *lamium*.
Bequaert 154, *pubescens* (BR); 1781, *owariensis* (BR); 1813, *madagascariensis* (US); 1905, *owariensis* (BR); 2640, *cf. vogeliana* (BR); 2927, *owariensis* (BR); 3934, *kirungae* (BR); 4836, *lamium* (BR); 5926, *kirungae* (BR); s.n. *owariensis* (US).
Bernardi 8677, *lamium* (K).
Bidgood & Keeley 334, *kirungae* (MO, UPS).
Bilolong 291, *owariensis* (P, YA); 317, *lamium* (K, YA).
Bille 1350, *lamium* (P).
Bingham 309, *pubescens* (LISC).
Binuyo FHI 45407, *vogeliana* (K).
Binuyo & Daramola FHI 35484, *owariensis* (K).
Bisset 1747, *kirungae* (SRGH).
Boissier 106, *lamium* (G).
Borhidi & Poçs 86763, *madagascariensis* (UPS).
Borhidi & Steiner 86427, *madagascariensis* (UPS).
Borhidi, Iversen, & Mziray 85214, *madagascariensis* (UPS).
Borhidi, Iversen, & Temu 86187, *madagascariensis* (UPS).
Bos 2310, *lamium* (WAG); 2359, *owariensis* (K); 2397, *owariensis* (WAG); 2444, *lamium* (K, WAG); 2552, *owariensis* (K, WAG); 3335, *lamium* (C, K, UPS, WAG, YA); 5387, *vogeliana* (C, K, MO, PRE, WAG, YA); 5626, *owariensis* (WAG).
Bos, van der Laan & Nzabi 10696, *debilis* (BR, WAG); 10755, *vogeliana* (K, US, WAG).
Boughley 7, *vogeliana* (K); 18882, *lamium* (K); GC11188, *owariensis* (K).
Bouxin 420, *owariensis* (BR); 799, *kirungae* (PRE); 1577, *madagascariensis* (BR).
Bouxin & Radoux 625, *kirungae* (BR).
Bowditch 374, *owariensis* (BM).
Brass 17021, *oligantha* (NY); 17042, *oligantha* (K, MO, NY); 17442, *riparia* (BM, MO, NY, US, SRGH); 17942, *pubescens* (MO, US, NY).
Braun 47, *vogeliana* (BM); 1316, *madagascariensis* (BM); 1925, *cf. lamium* (M); s.n. *owariensis* (M).
Brenan 8458, *owariensis* (K); 8534, *owariensis* (K).
Breteler 5303, *lamium* (M, MO, PRE, WAG).
Breteler & de Wilde 187, *debilis* (MO, WAG).
Breteler et al. 283, *owariensis* (K).
Bridson 610, *madagascariensis* (K, MO).
Bridson & Lovett 544, *kirungae* (MO).
Brodhurst-Hill 693, *owariensis* (Z).
Brown 2107, *owariensis* (MU).
Brown & Brown 33a, *lamium* (US); 316/b *lamium* (US).
Bruut 167, *owariensis* (K).
Brynaert 406, *pubescens* (BR).
Bunting s.n., *lamium* (BM, MO).
Burbidge 473, *owariensis* (K).
Burrows 769, *kirungae* (SRGH).
Burt 9, *lamium* (K); B16, *owariensis* (K).
Burt Davy 1228, *kirungae* (FHO).
Butayo s.n., *owariensis* (BM).
Butmer 353, *owariensis* (W).
Cambridge Congo Expedition 146, *kirungae* (BM, LISC, US).
Cardosode Matos 152, *owariensis* (LISC).
Carmichael 102, *kirungae* (FHO).
Carpenter 312, *owariensis* (K).
Carvalho 2359, *vogeliana* (K); 2445, *lamium* (BM, K, MO, S); 3766, *owariensis* (K, MO).
Casas 11471, *owariensis* (K); 11723, *owariensis* (K, MO); 11790, *owariensis* (K).
Chaloner 342c *owariensis* (K).
Chapman HNC191, *owariensis* (K); 827, *oligantha* (BM); 5053, *owariensis* (K); 5141, *owariensis* (K); 5258, *owariensis* (K).
Chapman & Chapman 8862, *kirungae* (E, FHO, MO, PRE); 9271, *kirungae* (E, FHO, MO).
Chase 854, *kirungae* (US); 2547, *pubescens* (BM); 2801, *pubescens* (BM); 2977, *kirungae* (MO); 6634, *kirungae* (S).
Chevalier 22, *owariensis* (P); 6296, *vogeliana* (K); 13362, *owariensis* (P); 22421, *owariensis* (P).
Chikuni & Tawakali 267, *kirungae* (MO).
Chipp 560, *owariensis* (K).
Christiansen 554, *madagascariensis* (BR).
Cole EAC187, *lamium* (K); 2394, *lamium* (K).
Coll. ign s.n., *kirungae* (WAG).
Compere 40321, *owariensis* (BR).
Cook 153, *lamium* (US).
Copley B1188, *lamium* (G).
Cours 4149, *madagascariensis* (P).
Cremers 1138, *lamium* (G).
Cribb & Grey-Wilson 10104, *madagascariensis* (DSM).
Croat 53479, *lamium* (K, MO).
Crockewit 249, *kirungae* (WAG).
Cudjoe 161, *lamium* (WAG).
Cultivated s.n., *owariensis* (P).
Cummins 245, *owariensis* (K).
Cunningham s.n., *madagascariensis* (LISC).
Dale U60, *kirungae* (S); 3208, *owariensis* (BR, FHO); 15538, *owariensis* (G).
Dalziel 148, *owariensis* (C, E, K, M, MO, PRE); 149, *lamium* (C, E, K, M, MO); 994, *lamium* (K); 1139, *owariensis* (K); 8232, *owariensis* (US); 8233, *owariensis* (K).
Daramola FH62407, *owariensis* (K); FHI 40467, *owariensis* (K); FHI 40574, *owariensis* (K); FHI 72304, *lamium* (K, MO).
Daramola & Adebunsi FHI 38430, *lamium* (K).
Daramola & Enwiogbon FHI 32774, *owariensis* (K).
Darker s.n., *lamium* (MO, NY).
Darko 897, *owariensis* (K).
Davies 643, *kirungae* (H, SRGH); 1426, *pubescens* (MO).
Davis & Jeffrey 186, *debilis* (K).
Dawkins D616, *lamium* (BM); 762, *madagascariensis* (BM).
de Brie s.n., *owariensis* (BR).
de Kruif 850, *owariensis* (WAG).
de Wilde 280, *lamium* (K, WAG, Z); 641, *lamium* (WAG); 859, *owariensis* (WAG); 7543, *lamium* (K, WAG); 7544, *owariensis* (WAG); 7635, *debilis* (WAG, YA); 8522, *lamium* (WAG, YA); 9415, *madagascariensis* (C, DSM, ETH, MO, UPS, WAG).

- de Wilde, Arends & Groenendijk* 3, *vogeliana* (WAG); 95, *vogeliana* (WAG).
- de Wilde & de Wilde-Duyffes* 1130, *vogeliana* (K, MO, YA); 2072, *debilis* (BR, K, MO, SRGH, WAG, YA, Z); 9415, *madagascariensis* (UPS, WAG); 10768, *grottanellii* (MO, WAG).
- de Wilde & Voorhoeve* 3772, *lamium* (K).
- de Wilde, de Wilde & de Wilde-Duyffes* 1152, *owariensis* (MO, PRE, WAG, YA); 3912, *owariensis* (H, MO, WAG); 4146, *owariensis* (K, WAG); 4198, *owariensis* (WAG); 4513, *owariensis* (WAG); 4557, *owariensis* (WAG).
- de Wilde et al.* 133, *debilis* (WAG).
- de Witte* 1434, *kirungae* (BR); 1508, *kirungae* (BR); 1539, *kirungae* (BR); 3986, *pubescens* (BR, K); 9697, *owariensis* (BR); 10747, *kirungae* (MO); 10872, *owariensis* (BR); 11065, *kirungae* (MO); 11640, *kirungae* (BR); 11862, *owariensis* (BR); 12148, *kirungae* (C); 12437, *owariensis* (BR); 12681, *madagascariensis* (BR); 12827, *cf. vogeliana* (BR, MO); 12907, *owariensis* (BR, MO); 12919, *owariensis* (BR).
- Decary* 2047, *madagascariensis* (P); 7782, *pubescens* (P); 8208, *pubescens* (MO, NY); 14.278, *madagascariensis* (P); s.n., *madagascariensis* (US).
- Deighton* 356, *owariensis* (K); 1419, *lamium* (BM, K, MO); 3571, *owariensis* (K); 5169, *lamium* (K); 5897, *owariensis* (K); 6141, *lamium* (K); 6152, *lamium* (K); 1419, *lamium* (K).
- Demeuse* 23, *owariensis* (BR).
- Denoulin* 61, *lamium* (K).
- Dennett* 34, *owariensis* (K).
- Dent Young* 194, *lamium* (K).
- Devred* 297, *owariensis* (BM, BR); 3429, *cf. vogeliana* (BR).
- Dinklage* 2624, *lamium* (H).
- Don* s.n., *vogeliana* (BM); s.n., *owariensis*.
- Dowsette-Lemaire* 999, *kirungae* (MAL).
- Drummond & Hemsley* 4556, *madagascariensis* (S); 4584, *lamium* (S); s.n., *kirungae* (S).
- Dschang College* 1712, *owariensis* (K).
- Duchesne* 13, *lamium* (BR).
- Dujardin* 409, *owariensis* (BR).
- Dümmer* 247, *owariensis* (MO, US, Z); 587, *cf. owariensis* (P, US); 1048, *lamium* (US, Z); 3975, *madagascariensis* (US).
- Dundas* FHI 15323, *lamium* (K).
- Dunlap* 25, *owariensis* (K).
- Dusen* s.n., *lamium* (S).
- Eckendorf* 73, *owariensis* (P).
- Eggeling* 402, *lamium* (FHO); 1380, *lamium* (FHO); 1487, *owariensis* (FHO); 3323, *vogeliana* (K).
- Eijnatten* 2130, *lamium* (WAG).
- Ekwuno, Osanyinlusi & Okoro* 124, *owariensis* (MO).
- Elskens* 7, *owariensis* (BR); 76, *owariensis* (BR); s.n., *owariensis* (BR).
- Emwiogbon* FHI 87191, *lamium* (MO); 66079, *owariensis* (K).
- Emwiogbon & Osanyinlusi* FHI 87313, *lamium* (MO).
- Ensermu et al.* 745, *grottanellii* (ETH); 821, *grottanellii* (ETH).
- Ensermu & Zerihun* 649, *grottanellii* (C, ETH).
- Espirito-Santo* 67, *lamium* (PRE); 68, *vogeliana* (BM); 3870, *lamium* (LISC); 4312, *lamium* (LISC); 4727, *lamium* (LISC); 4298, *vogeliana* (LISC); 5118, *lamium* (LISC).
- Etuge & Thomas* 442, *owariensis* (K, MO); 451, *owariensis* (MO).
- Evrard* 2681, *lamium*; 6002, *vogeliana* (BR, K); 6004, *vogeliana* (PRE).
- Exell* 88, *vogeliana* (BM, K); 100, *vogeliana* (BM, K); 533, *lamium* (K).
- Exell & Mendonça* 3139, *owariensis* (BM); 3149, *owariensis* (BM); 3193, *owariensis* (BM).
- Eyles* 3601, *kirungae* (SRGH).
- Fabrigues* 3306, *lamium* (P).
- Faden & Faden* 77/919, *kirungae* (BR, US, WAG).
- Fairbairn* 1934, *owariensis* (MO).
- Fanshawe* F11642, *kirungae* (FHO).
- Farquhar* 42, *lamium* (K).
- Farron* 4085, *vogeliana* (P); 4582, *vogeliana*.
- Fay* 1844, *lamium* (K); 6055, *lamium* (K, MO).
- Federicq* 8116, *kirungae* (BR).
- Figueiredo & Arriegas* 31, *lamium* (FHO, K, LISC); 32, *vogeliana* (K); 33, *vogeliana* (FHO, K, LISC); 66, *vogeliana* (K).
- Fischer* 81, *lamium* (K).
- Fishlock* 16, *lamium* (K); 55, *owariensis* (BM, K).
- Flanigan* 193, *owariensis* (NY).
- Florence* 1706, *vogeliana* (P).
- Fotius* 2485, *owariensis* (P, YA).
- Frederick* 8439, *madagascariensis* (BR); 9491, *owariensis* (BR).
- Friedberg* 1, *vogeliana* (K).
- Friis & Vollesen* 58, *kirungae* (C); 483, *owariensis* (C); 612, *vogeliana* (C); 613, *madagascariensis* (C); 619, *lamium* (C); 1299, *owariensis* (C).
- Friis et al.* 1677, *grottanellii* (C); 1882, *madagascariensis* (C, ETH); 1908, *madagascariensis* (C, ETH); 6023, *grottanellii* (ETH); 6041, *grottanellii* (ETH).
- Friis, Gilbert & Vollesen* 4109, *madagascariensis* (ETH, UPS).
- Friis, Hounde & Jacobsen* 369, *madagascariensis* (ETH).
- Froment* 385, *owariensis* (BR).
- Garley* 464, *kirungae* (LISC).
- Garrett* s.n., *owariensis* (K).
- Gassy Leon* 2002, *lamium* (K).
- Gbile* 27, *lamium* (MO).
- Geerling & Bockdam* 1533, *lamium* (C, MO, WAG); 1739, *lamium* (K, MO, WAG); 1859, *owariensis* (C, MO, WAG); 1951, *lamium* (C, MO, WAG).
- Gelinger* 2869, *kirungae* (Z).
- Gentry* 11720, *madagascariensis* (MO).
- Geo Watt* 7049, *lamium* (BM, MO).
- Gerard* 1954, *lamium* (K); 3626, *lamium* (K); 5341, *lamium* (BR, K).
- Gereau et al.* 5561, *lamium* (K); 5629, *owariensis* (K); 5657, *owariensis* (K).
- Germain* 1952, *madagascariensis* (PRE); 3915, *kirungae* (BR); 4934, *madagascariensis* (BR); 7826, *madagascariensis* (BR); 8141, *owariensis* (BR).
- Gilbert & Mexfin* 6612, *kirungae* (PRE).
- Gilli* 519, *kirungae*.
- Gocker* 2, *vogeliana* (MO, US).
- Goldsmith* 54161, *kirungae* (MO).
- Gomes & Sousa* 4137, *riparia* (PRE).
- Goosens* 1313, *owariensis* (BR); 2369, *owariensis* (BR); 6030, *lamium* (K).
- Gossweiler* 131, *lamium* (BM); 500B, *owariensis* (BM); 1048, *owariensis* (BM).
- Goudot* s.n., *madagascariensis* (G).
- Greenway & Brenan* 8044, *pubescens* (PRE).
- Greenway & Eggeling* 8394, *kirungae* (PRE); 8594, *kirungae* (FHO).
- Greenway & Farquhar* 8634, *madagascariensis* (NY, PRE).
- Greenway & Kanuri* 12107, *madagascariensis* (PRE).
- Greve* 26, *pubescens* (P).
- Groenendijk & Dunge* 466, *riparia* (SRGH).
- Guile* 1733, *owariensis* (MO).
- Guinea* 482, *vogeliana* (K).
- Gutzwiller* 841, *madagascariensis* (BR); 1612, *madagascariensis* (BR).
- H.V.L.* P652, *lamium* (K).
- Haaren* 2483, *lamium* (G).
- Hall-Martin* 819, *pubescens* (PRE).
- Hallam* 128, *lamium* (K).
- Halle* 2382, *owariensis* (P); 3130, *owariensis* (P); 3337, *vogeliana* (P); 3282, *owariensis* (P); 4058, *vogeliana* (K, P).
- Halle & Villiers* 4626, *lancifolia* (P); 4806, *debilis* (K); 4897, *debilis* (P); 5047, *debilis* (P).
- Hamblet* 108, *owariensis* (K); 696, *lamium* (K, SRGH).
- Hanke* 415, *lamium* (G, Z).
- Hansen* 713, *lamium* (C); 937, *kirungae* (C).
- Harley* 678, *lamium* (K); 1631, *owariensis* (K).
- Harris* 116, *kirungae* (DSM).
- Harris & Mwasumbi* 2462, *madagascariensis* (DSM).
- Harris & Poçs* 3227, *pubescens* (DSM); 3274, *kirungae* (DSM, US).
- Head* 16, *owariensis* (K); 60, *lamium* (K).
- Hedin* s.n., *owariensis* (P).
- Hedré, Iversen, Mziray & Pocs* 84118, *madagascariensis* (UPS).
- Hendrickx* 77, *owariensis* (BR); 4067, *owariensis* (PRE); 7226, *owariensis* (BR).

- Hepburn 71, *lamium* (K).
 Hepper 1094, *owariensis* (K); 1151, *lamium* (K); 1332, *owariensis* (K, S); 1651, *owariensis* (K, S, UPS); 1972, *owariensis* (FHO, K, S, UPS); 6806, *lamium* (K).
 Hildebrandt 3901, *madagascariensis* (BM, G, M, W, Z).
 Holst 3316, *madagascariensis* (H); 4216, *madagascariensis* (G, US, Z).
 Hornby 2773, *kirungae* (PRE).
 Howard UTT 16, *lamium* (C).
 Humbert 2670, *pubescens* (BM, G, US); 11390, *pubescens* (P); 20729, *madagascariensis* (P); 23090, *madagascariensis* (P).
 Humbert & Swingle 4385, *pubescens* (S).
 Humboldt 645, *madagascariensis* (P).
 Hutchinson & Metcalfe 122, *owariensis* (K).
 Irian FHI 23095, *lamium* (K).
 Irvine 4881, *owariensis* (K); 5147, *owariensis* (K).
 Irving s.n., *lamium* (K).
 Iversen & Steiner 86667, *madagascariensis* (UPS).
 Jackson 1023, *madagascariensis* (BM); 1144, cf. *grottanellii* (BM, MO).
 Jacques-Felix 1246, *owariensis* (K, P); 1188, *lamium* (P); 2600, *owariensis* (P); 8087, *lamium* (K, YA); 9135, *vogeliana* (K, YA); 9136, *lamium* (P, YA).
 Jaeger 7770, *lamium* (K).
 Jansen 975, *lamium* (WAG); 1062, *lamium* (WAG); 2207, *lamium* (WAG); 2398, *lamium* (WAG); 2514, *lamium* (WAG).
 Jardin Butenzorg 68, *owariensis* (P).
 Jeffrey 109, *vogeliana* (K).
 Jolunson 965, *lamium* (K).
 Johnston s.n., *lamium* (K).
 Jones 127, *owariensis* (K).
 Jongkind, Schmitt & Abbw 1799, *owariensis* (K).
 Jordan 375, *lamium* (K).
 Jungner 181, (S, UPS); 229, *lamium* (UPS); 248, *lamium* (S, UPS); 258, *vogeliana* (UPS).
 Juniper, Jefford & Mgaza 256, *owariensis* (MO).
 Kalurananga, Kibuwa & Mungai 2631, *owariensis* (M, UPS).
 Kanneh 601, *lamium* (MO, NY, UPS).
 Kassner (1)2908, *vogeliana* (E, H, Z); 3113, *kirungae* (H).
 Katende 831, *vogeliana* (BM); K522, *kirungae*; 969, *lamium* (MO); K2503, *kirungae* (MO); 2824, *vogeliana* (MO).
 Kaudern s.n., *pubescens* (S).
 Kaunda & Usi 429, *riparia* (MAL).
 Kayombo 1072, *owariensis* (MO).
 Keay FHI 28233, *owariensis* (K); FHI 28264, *owariensis* (K).
 Keay & Keay FHI 20068, *lamium* (FHO).
 Keay & Onochie FHI 20245, *lamium* (K).
 Kennedy 1571, *lamium* (FHO, K, US); 2672, *lamium* (K).
 Kerfoot 3735, *owariensis* (PRE); 4374, *kirungae* (SRGH).
 Kersting A108, *owariensis* (BM).
 Kibuwa 5191, *madagascariensis* (UPS).
 King 39B *lamium* (K); I14B *owariensis* (K).
 Kitson s.n., *owariensis* (BM, MO, NY).
 Koechlin 2891, *owariensis* (P).
 Kruif 850, *owariensis* (WAG).
 La Croix 3122, *pubescens* (MO); 3114, *riparia* (MO); 4083, *kirungae* (MO); 4600, *kirungae* (MO).
 Lamb 66, *owariensis* (K); s.n., *lamium* (UPS).
 Laminon 78/321, *madagascariensis* (BR).
 Lane Poole 392, *lamium* (K).
 Lang Brown 9, *kirungae* (FHO); 81, *owariensis* (FHO).
 Latilo 97, *owariensis* (K); FHI 43460, *lamium* (K); FHI 67539, *lamium* (K).
 Latilo & Daramola FHI 28926, *owariensis* (FHO, K); FHI 28969, *owariensis* (K); FHI 28992, *owariensis* (FHO).
 Latilo & Fagbemi FHI 64782, *lamium* (K).
 Lawlor & Hall 659, *lamium* (K).
 Le Testu 9, *owariensis* (BM); 1010, *owariensis* (FHO); 3541, *owariensis* (BM, P); 3557, *lamium* (K); 5943, *lancifolia* (BM, BR, P); 6431, *madagascariensis* (BM, MO); 6478, *debilis* (BM, P); 8853, *madagascariensis* (BM, P); 9135, *debilis* (BM); s.n., *lamium* (BM); 9395, *owariensis* (BR).
 Leach & Brunton 10069, *kirungae* (SRGH).
 Leach & Cannell 14324, *pubescens* (LISC).
 Leach & Schelpe 11470, *kirungae* (LISC, SRGH).
 Lebrun 309, *vogeliana* (BR); 459, *owariensis* (BR); 1858, *madagascariensis* (BR); 3278, *lamium* (K); 3515, *lamium* (K).
 Leeuwenberg 1808, *lamium* (K); 2948, *owariensis* (WAG); 4198, *owariensis* (P, WAG); 6238, *vogeliana* (WAG); 6494, *lamium* (K, YA); 6496, *vogeliana* (K, LISC, MO, PRE, YA); 6560, *debilis* (K, LISC, MO, PRE, WAG, YA); 6870, *vogeliana* (K, LISC, MO, WAG, YA); 6964, *lamium* (LISC, MO, PRE); 6967, *vogeliana* (K, YA); 7100, *vogeliana* (BM, C, K, LISC, WAG); 7655, *owariensis* (K, LISC, MO, WAG, YA); 8206, *lamium* (H, LISC, MO, UPS, WAG); 8419, *vogeliana* (H, K, LISC, M, MO, PRE, UPS, WAG, YA); 8554, *owariensis* (MO, PRE, WAG, YA); 8994, *lancifolia* (C, H, LISC, PRE, UPS, WAG, YA); 6870); 9244, *owariensis* (LISC, PRE, UPS, WAG, YA); 9245, *owariensis* (H, LISC, MO, PRE, UPS, WAG, YA); 10628, *vogeliana* (K, MO, WAG, YA).
 Lejoly 2281, *kirungae* (BR); 84/409, *kirungae* (BR).
 Lely 129, *owariensis* (FHO, K); 469, *lamium* (K); 652, *lamium* (MO).
 Leonard 771, *lamium* (MO); 1678, *kirungae* (BR).
 Letouzey 1178, *madagascariensis* (H); 3561, *owariensis* (P, YA); 5472, *debilis* (K, P, YA); 5474, *vogeliana* (K); 5666, *lamium* (P); 7920, *lamium* (K, NY, YA); 8159, *debilis* (K, P, YA); 8241, *lamium* (K, P, YA); 8393, *lamium* (K, YA); 8446, *madagascariensis* (P); 10229, *debilis* (K, P); 10909, *owariensis* (K, YA); 13252, *owariensis* (P, YA); 15340, *vogeliana* (P).
 Lewalle 795, *kirungae* (BR); 3575, *kirungae* (BR, NY); 3640, *kirungae* (BR, G); 3778, *kirungae* (BR, NY); 3783, *madagascariensis* (BR, G, SRGH); 3795, *owariensis* (BR); 5613, *lamium* (K); 5740, *kirungae* (BR).
 Liben 2989, *lamium* (PRE).
 Linder 859, *lamium* (K, MO, WAG); 3441, *owariensis* (K, PRE).
 Longfield 21, *owariensis* (BM); 66, *kirungae* (BM, US).
 Louis 118, *vogeliana* (WAG); 1307, cf. *vogeliana* (BR, MO); 1672, *owariensis* (BR); 2077, *vogeliana* (WAG); 2161, *debilis* (WAG); 4404, *lamium* (K); 4632, *kirungae* (BR); 7656, *madagascariensis* (BR); 8993, *owariensis* (BR, PRE); 10839, *madagascariensis* (C); 10841, cf. *vogeliana* (BR); 12194, *madagascariensis* (BR, C, MO); 12350, *owariensis* (BR);
 Loveridge 25, *vogeliana* (K); 26, *madagascariensis* (MO).
 Lovett & Lovett 2062, *kirungae* (MO).
 Lowe 1804, *lamium* (K); 1809, *lamium* (K); 2955, *owariensis* (K).
 Ludanga 1337, *pubescens* (C).
 Luxen 373, *owariensis*.
 Lye 1657, *owariensis* (MHU); 2768, *lamium* (UPS); 5555, *kirungae* (SRGH).
 M. I. B. 629, *owariensis* (BR).
 Mabblerley 1403, *kirungae* (DSM, K).
 MacGregor 265, *lamium* (K); 333, *lamium* (K); 402, *owariensis* (K).
 Magnus s.n., *owariensis* (H).
 Maitland 110, *vogeliana* (K); 199, *owariensis* (K); 207, *owariensis* (K); 757, *vogeliana* (K); 1619, *lamium* (K).
 Malaisse & Goetghebeur 242, *owariensis* (BR).
 Manktelow, Steiner & Amponsah 89, *vogeliana* (UPS).
 Mann 36, *vogeliana* (K); 1688, *lancifolia* (K); 1861, *lamium* (K); 1959, *owariensis* (K).
 Manning 67, *lamium* (K, MO); 398, *lamium* (K, MO); 441, *vogeliana* (MO); 1045, *owariensis* (MO); 1046, *lamium* (K, MO); 1049, *owariensis* (K, MO).
 Marmo 114, *owariensis* (K); 251, *lamium* (K).
 Mathey & Scholz 312, *lamium* (K).
 Mbago 1030, *owariensis* (DSM).
 McClintock 222, *owariensis* (K).
 McEderly 7627, *owariensis* (BM).
 Mearns 2465, *owariensis* (US).
 Meijer 15307, *debilis* (MO).
 Meikle 590, *lamium* (K); 953, *lamium* (K).
 Melville & Hooker 85, *lamium* (K); 357, *lamium* (K).
 Mendonça 680, *riparia* (LISC); 1219, *riparia* (LISC); 2110, *kirungae* (LISC).

- Methuen* 80, *kirungae* (LISC).
Meurillon 402, *lamium* (K, P); 521, *owariensis* (P); 859, *owariensis* (BR); 886, *owariensis* (BR); 1998, *vogeliana* (K).
Meurillon et al., 1970, *lamium* (K); 2031, *lamium* (K).
Meyer 7995, *grottanellii* (US); 8131, *madagascariensis* (US).
Michel 2370, *owariensis* (MO); 5522, *kirungae* (BR).
Migeod 27, *owariensis* (K); 359, *owariensis* (BM); *Migeod* s.n., *owariensis* (BM).
Mildbraed 3866, *vogeliana* (H); 4147, *madagascariensis* (H); 5487, *owariensis* (BR); 5782, *owariensis* (H); 7028, *vogeliana* (H); 7126, *madagascariensis* (H); 7353, *owariensis* (K).
Milne 140, *lamium* (W).
Mocquery 9, *lamium* (G, Z); 96, *vogeliana* (G, Z); 115, *owariensis* (G, Z).
Monod 11681, *lamium* (BM); 11718, *vogeliana* (BM); 11857, *vogeliana* (BM); 11881, *vogeliana* (BM).
Montiero 46, *riparia* (LISC).
Montiero & Murta 198, *owariensis* (PRE); 205, *owariensis* (PRE).
Montiero, Santos & Murta 205, *owariensis* (PRE).
Mooney 6071, *madagascariensis* (ETH, K, S); 6725, *grottanellii* (ETH); 6890, *grottanellii* (S).
Moriarty 18, *kirungae* (MAL).
Morton A36, *vogeliana* (K); A114, *lamium* (K); 327, *lamium* (BM, FHI, GC, K, SL, WAG); K416, *owariensis* (K, WAG); A1032, *lamium* (K); A1643, *lamium* (K); *Morton* GC8213, *vogeliana* (K); GC9378, *lamium* (K).
Morton & Gledhill SL242, *owariensis* (K).
Morton & Jarr SL2394, *lamium* (K).
Mucke 257, *madagascariensis* (PRE).
Mullenders 2087, *lamium* (BR).
Müller 802, *kirungae* (SRGH); 2353, *kirungae* (LISC).
Mwasumbi 11874, *kirungae* (DSM).
Mwasumbi & Munyenyembe 13883, *pubescens* (DSM).
Nannan 33, *owariensis* (BM); 164, *lamium* (BM, BR).
Napper 1515, *lamium* (PRE).
Nemba & Mambo 622, *vogeliana* (MO).
Newberry s.n., *lamium* (K).
Newbold & Harley 4289, *owariensis* (MO).
Newman & Whitmore 574, *kirungae* (NY).
Nkongmeneck 201, *owariensis* (P, YA).
Nolde 227, *owariensis* (BM).
Norman 103, *owariensis* (S); s.n., *madagascariensis* (MHU).
Offerman et al. 648, *lamium* (BR, K).
Okafor FHI 35870, *lamium* (K).
Oldeman 108, *lamium* (K, WAG).
Onochie FHI 34064, *lamium* (K); FHI 40410, *owariensis* (K); FHI 40416, *lamium* (K).
Osmaston 2497, *owariensis* (BM).
Overlaet 544, *madagascariensis* (BR); 1052, *madagascariensis* (BR).
Page-Wilkes 594, *kirungae* (MO).
Patel & Kwatha 2856, *pubescens* (MAL).
Paulo 646, *kirungae* (BR).
Pawek 6978, *kirungae* (MO, PRE, SRGH, UPS); 10135, *kirungae* (MO); 11717, *pubescens* (LISC, MO, SRGH); 12984, *oligantha* (K, LISC, MAL, MHU, MO, SRGH).
Pearson 2273, *owariensis* (BM).
Perdue & Kibuwa 9242, *kirungae* (LISC); 9435, *kirungae* (LISC).
Perrier 1066, *pubescens* (P); 9227, *madagascariensis* (P); 9261, *madagascariensis* (P); 9416, *pubescens* (P); 9345, *madagascariensis* (P).
Peter & Tuley 58, *owariensis* (K).
Peyre de Fabrigues 3306, *lamium* (P).
Phillips 2836, *oligantha* (MO); 2846, *kirungae* (MO, Z); 3507, *kirungae* (MAL, MO).
Pierlot 146, *owariensis* (PRE); 1649, *madagascariensis* (BR).
Pilz 2069, *lamium* (K); 2190, *lamium* (K); 2658, *lamium* (K).
Pimenta s.n., *kirungae* (LISC).
Plowes 2261, *kirungae* (LISC, SRGH); 2456, *kirungae* (LISC, PRE).
Poços et al. 8722, *stenopteris* (UPS).
Pole Evans & Erens 1796, *kirungae* (BR, E).
Pope 1987, *pubescens* (MO, SRGH).
Poulsen et al. 523, *kirungae* (C, FHO, K, MU).
Preuss s.n., *owariensis* (BM); 998, *vogeliana* (BM); 1029, *owariensis* (BM, M).
Price & Evans 69, *debilis* (K); 71, *debilis* (K).
Procter 428, *owariensis* (PRE).
Puff & Ensermu 861107-4/6, *grottanellii* (ETH).
Pyne 11, *lamium* (K); 109, *owariensis* (K); 138, *lamium* (K, P, S).
Quintas 1235(88) *lamium* (BM, Z).
Rainano, Matos & Figueira 254, *owariensis* (LISC).
Rakotozafy 287, *madagascariensis* (P).
Ratabu 17, *madagascariensis* (MO).
Ratray s.n., *lamium* (K).
Raynal 11964, *vogeliana* (P); 20477, *kirungae* (K).
Raynal & Raynal 9719, *debilis* (P, YA); 10009, *vogeliana* (P, YA); 12167, *owariensis* (P, YA); 12966, *owariensis* (P, YA).
Reekmans 1136, *madagascariensis* (BR); 1986, *kirungae* (MO); 5237, *kirungae* (C, MO); 5918, *lamium* (K, MO, PRE); 7028, *lamium* (K, MO); 8288, *owariensis* (MO, PRE, SRGH); 9060, *lamium* (K, MO); 9408, *kirungae* (K, MO, UPS); 10009, *kirungae* (K, MO); 10017, *kirungae* (K, MO, PRE, UPS); 10073, *kirungae* (K, MO, UPS); 10604, *kirungae* (K, MO, PRE, S, UPS).
Reitsma & Reitsma 1048, *vogeliana* (WAG).
Reitsma, Reitsma & Louis 1880, *debilis* (NY, WAG).
Reynders 411, *kirungae* (PRE).
Richards 3108, *owariensis* (BM, MO, NY); 12983, *kirungae* (SRGH); 24663, *madagascariensis* (C, M).
Robertson 62, *lamium* (BM).
Roberty 6590, *lamium* (G, Z); 6652, *owariensis* (G); 6946, *lamium* (G, Z); 10695, *owariensis* (G, Z); 12613, *lamium* (G, MO, Z); 13020, *vogeliana* (G); 15849, *lamium* (G); 15991, *owariensis* (G); 16148, *owariensis* (G); 16202, *lamium* (G); 16210, *owariensis* (G, Z); 16412, *owariensis* (G).
Robevazalia 11530, *madagascariensis* (P).
Robson & Fanshawe 537, *kirungae* (LISC, SRGH).
Robyns 151, *owariensis* (BR); 2098, *owariensis* (BR).
Rodgers-Hall 1484, *kirungae* (DSM).
Rosevear 41-29, *lamium* (K); 68-31, *owariensis* (FHO); 82-29, *lamium* (K).
Saeger 1431, *lamium* (C, MO).
Safy 6312, *madagascariensis* (P).
Salubeni 1485, *oligantha* (SRGH); 1487, *oligantha* (MAL, PRE, SRGH); 1489, *kirungae*; 1803, *pubescens* (MO, SRGH); 1842, *pubescens* (MO).
Salubeni & Kaunda 4523, *pubescens* (MAL).
Salubeni & Tawakali 2334, *riparia* (MO).
Samai 579, *lamium* (K).
Sanford 4617, *lamium* (MO); 5812, *lancifolia* (K).
Satuble 953, *lamium* (G).
Savory FHI 36599, *owariensis* (K).
Savory & Keay FHI 25015, *owariensis* (K); FHI 25056, *owariensis* (K); FH25017, *owariensis* (K).
Saxer 248, *lamium* (G, K, Z).
Scaetta 3112, *lamium* (P); 3284, *lamium* (P).
Schlieben 1358, *kirungae* (G, M, LISC, S, Z); 2767, *kirungae* (G, S, Z); 4068, *stenopteris* (LISC, MO, PRE); 4069, *madagascariensis* (G, H, LISC, M, P, S, Z); 4108, *kirungae* (G, LISC, M, S, Z); 5323, *pubescens* (G, H, LISC, M, MO, PRE, S, Z).
Schmidt et al. 2090, *lamium* (K).
Schnell 6513, *lamium* (K).
Schweicht 2423, *kirungae* (LISC, PRE).
Scott Elliot 3990, *owariensis* (BM); 3990a, *owariensis* (K).
Scurlock 17, *lamium* (K).
Seret 97, cf. *vogeliana* (BR); 346, *vogeliana*; 716, *owariensis* (BR).
Sharland 362, *owariensis* (K); 1155, *owariensis* (K); 1202, *owariensis* (K); 1411, *lamium* (K); 1736, *owariensis* (K); 1802, *lamium* (K).
Sharpe B8833, *kirungae* (G).
Shaw 26, *owariensis* (K).
Sita 670, *lamium* (P).
Small 212, *lamium* (K); 243, *lamium* (K, P).
Smevers 32, *kirungae* (BR); 54, *lamium*.

- Smith s.n., *owariensis* (K).
 Smythe 240, *owariensis* (K).
 Snowden 954, *kirungae* (G, MO); 1847, *owariensis* (G).
 Soyaux 118, *owariensis* (M, W); 454, *vogeliana* (E, H, US).
 Stanton 38, *owariensis* (BM, SRGH).
 Stauble 952, *lamium* (G).
 Staudt 240, *debilis* (G, K, NY, S, WAG).
 Stauffer 46, *kirungae* (PRE, UPS, Z).
 Stolz 152, *kirungae* (G, M, MO, NY, S, W, Z).
 Stone 63, *lamium* (K); 86, *lamium* (K).
 Strid 2916, *kirungae* (S).
 Stubbing 200, *lamium* (K).
 Swarbrick 293, *vogeliana* (E, YA); TS2822, *lamium* (K).
 Synge 31395, *kirungae* (BM, MO, S, US).
 Talbot s.n., *lamium* (K, Z); 981, *lamium* (BM, K, Z); 993, *owariensis* (K); 1393, *owariensis* (MO); 1912, *owariensis* (MO); 2000, *lancifolia* (BM, K).
 Talbot & Talbot s.n., *owariensis* (K); 1270, *owariensis* (K).
 Taton 1172, *lamium* (BR).
 Taylor s.n., *madagascariensis* (MO); 1660, *lamium* (BM, MO, S); 2477, *owariensis* (BM, MO); 2516, *owariensis* (BM); 3156, *kirungae* (BM, MO, S); 3203, *owariensis* (BM); 3284, *owariensis* (S); 3327, *madagascariensis* (BM, MO); 3384, *owariensis* (BM).
 Thera & Kaunda 313, *pubescens* (PRE).
 Thijsen 276, *lamium* (WAG).
 Thoen 4829, *pubescens* (BR).
 Thomas, A.S. 1595, *owariensis* (BM); 1768, *owariensis* (BM); 2845, *owariensis* (MO); 2952, *owariensis* (MO, PRE, YA).
 Thomas, D.W. 1722, *lamium* (K); 2091, *lamium* (K); 2096, *lamium* (S); 2320, *lamium* (K); 2502, *lamium* (BM, MO, NY); 2609, *vogeliana* (MO, YA); 2762? *lamium* (W); 2775, *lancifolia* (MO); 2845, *owariensis* (MO); 2935, *lamium* (K); 2952, *owariensis* (K, MO, PRE); D.W. 3790, *kirungae* (MO); 4381, *owariensis* (MO, YA); 7149, *owariensis* (MO); 9005, *owariensis* (MO).
 Thomas, D.W. & Macleod 5106, *owariensis* (MO); 5145, *owariensis* (MO).
 Thomas, D.W. & Mambo 4235, *lamium* (K, MO, PRE).
 Thomas, D.W., Mambo & Nemba 4987, *owariensis* (MO, NY).
 Thomas, D.W. & Nemba 4047, *lamium* (MO); 4048, *vogeliana* (K, MO, YA).
 Thomas, N.W. 102, *owariensis* (K); 2034, *owariensis* (K); 2285, *owariensis* (K).
 Thompson & Rawlins 1460, *lamium* (MO).
 Thulin & Mhoru 2904, *kirungae* (UPS); 3181, *kirungae* (MO, UPS).
 Tindall 29, *owariensis* (K).
 Tinley 2639, *pubescens* (LISC, MO, SRGH).
 Tisserant 1352, *lamium* (P); 2346, *lamium* (BM); 2743, *cf. vogeliana* (BM, P); 3167, *lamium* (BM, P); 3245, *owariensis* (P); 3556, *lamium* (LISC, P).
 Torre 486, *riparia* (LISC); 4586, *kirungae*; 35354, *kirungae* (LISC).
 Torre & Correia 15977, *kirungae* (LISC).
 Toussaint 2311, *cf. vogeliana* (BR).
 Troupin 392, *owariensis* (BR); 395, *owariensis* (BM); 1442, *lamium* (K); 2468, *vogeliana* (BR); 2986, *kirungae* (BR); 4580, *owariensis* (BR, K); 4711, *owariensis* (BR, K); 7523, *owariensis* (BR); 9332, *owariensis* (BR); 9393, *kirungae* (BR); 10371, *kirungae* (BR); 11058, *kirungae* (BR); 11723, *kirungae* (MO, US).
 Tufnell s.n., *owariensis* (BM).
 Tuley 1001, *lamium* (K); 1003, *owariensis* (K); 1934, *owariensis* (K).
 Tyres 339, *pubescens* (SRGH).
 Ujor FHI 30224, *lamium* (K).
 Usi & Kaunda 606, *pubescens* (MAL).
 van der Ben 648, *owariensis* (BR); 1120, *owariensis* (BR, SRGH).
 van der Laan 986, *debilis* (WAG).
 van der Veken 10350, *kirungae* (BR).
 van Harten 192, *lamium* (H, K, WAG).
 van Meer 303, *owariensis* (BM, MO, WAG).
 Vanden Hondt 58, *kirungae* (BR).
 Vanderijst s.n., *lamium* (BR).
 Verdcourt 1674, *kirungae* (PRE); 1683, *vogeliana* (K).
 Vermoesen 1852, *cf. vogeliana* (BR); 1854, *owariensis* (BM).
 Vogel 17, *lamium* (K).
 Vollesen 2392, *pubescens* (C).
 Voorhoeve 726, *owariensis* (WAG).
 Vuyk 330, *madagascariensis* (WAG).
 Watmough 707, *pubescens* (SRGH).
 Watt 7384, *vogeliana* (BM).
 Welwitsch 5149, *owariensis* (BM); 5150, *owariensis* (BM); 5182, *owariensis* (BM, G); 5205, *lamium* (BM).
 White 8520, *owariensis* (FHO); 13908, *kirungae* (FHO).
 Whyte s.n., *lamium* (K).
 Wild 3566, *kirungae* (NY).
 Williams s.n., *owariensis* (US); 33, *kirungae* (MO); 216, *kirungae* (LISC, SRGH).
 Winkler 505, *vogeliana* (Z).
 Wollaston s.n., *owariensis* (BM).
 Wright 2463, *lamium* (FHO).
 Wyld 679, *lamium* (BM).
 Yamada 261, *lamium* (K).
 Yates 35, *owariensis* (K).
 Young 651, *kirungae* (BM).
 Zenker 286, *owariensis* (C, MO, US, Z); 396, *lamium* (C, G); 513, *vogeliana* (K); 1104, *lamium* (BM, E, K).
 Zenker & Staudt 520, *owariensis* (S, Z).

SYSTEMATIC INDEX

Accepted names are in roman, and synonyms in italic; new names and principle references are in **bold**.

- Belantheria* Nees **83**
belvisiana Nees 83, 90
- Brillantaisia* P. Beauv. **83**
alata T. Anderson ex Oliv. 90
anomala Lindau 84
bagshawei S. Moore 104
bauchiensis Hutchinson & Dalziel 92
borellii Lindau 106
cicatricosa Lindau 95, 105
cicatricosa var. *kivuensis* Mildbr. 93
debilis Burkill 83, **101**, 102, 103
dewevrei De Wild. & Th. Dur. 92
didynama Lindau 106
eminii Lindau 97
fulva Lindau 106
grandidentata S. Moore 93
grottanellii Pichi-Sermoli, 83, **103**, 105
hirsuta T. Anderson 105
kirungae Lindau 84, **93**, 94
lamium (Nees) Benth. 83, **97**, 98
lancifolia Lindau 83, 99, 100, **101**
leonensis Burkill 92
- madagascariensis* T. Anderson ex Lindau 83, **104**
mahonii C.B. Clarke 92
majestica Wernham 104
molleri Lindau 95
nitens Lindau 92
 sensu Agnew 93
nyanzarum Burkill 92
oligantha Milne-Redhead 84, **86**, 88, 89
owariensis P. Beauv. 83, 84, **90**
 sensu Hook. 97
palisotii Lindau 97
patula T. Anderson 90
patula var. *welwitschii* Burkill 92
preussii Lindau 95
pubescens T. Anderson ex Oliv. 83, **84**, 85
pubescens var. *riparia* Vollesen & Brummitt 86
pubescens var. *rutenbergiana* (Vatke) Benoist 84
riparia (Vollesen & Brummitt) Sidwell 83, **86**, 87
rutenbergiana Vatke 84
salviiflora Lindau 90
schumanniana Lindau 95
soyauxii Lindau 95
- soyauxii sensu* Heine 101
spicata Lindau 104
stenopteris Sidwell 84, **89**, 90, 91
subcordata De Wild. & T. Durand 97
subcordata var. *macrophylla* de Wild. & Th. Dur.
 97
subulgurica Burkill 93
talbotii S. Moore 101
thwaitesii Cramer 106
ulugurica Lindau 93
verruculosa Lindau 104
vogeliana (Nees) Benth. 84, **95**, 96
- Hygrophila* 68
pubescens (T. Anderson ex Oliv.) Benoist 84
thwaitesii (Benth.) Heine 106
- Leucoraphis* Nees **83**
lamium Nees 97
vogeliana Nees 83, 95
- Plaesianthera* (C.B. Clarke) Livera 68, 106
thwaitesii (C.B. Clarke) Livera 106
- Ruellia* Baillon 83
grevei Baillon 83, 84